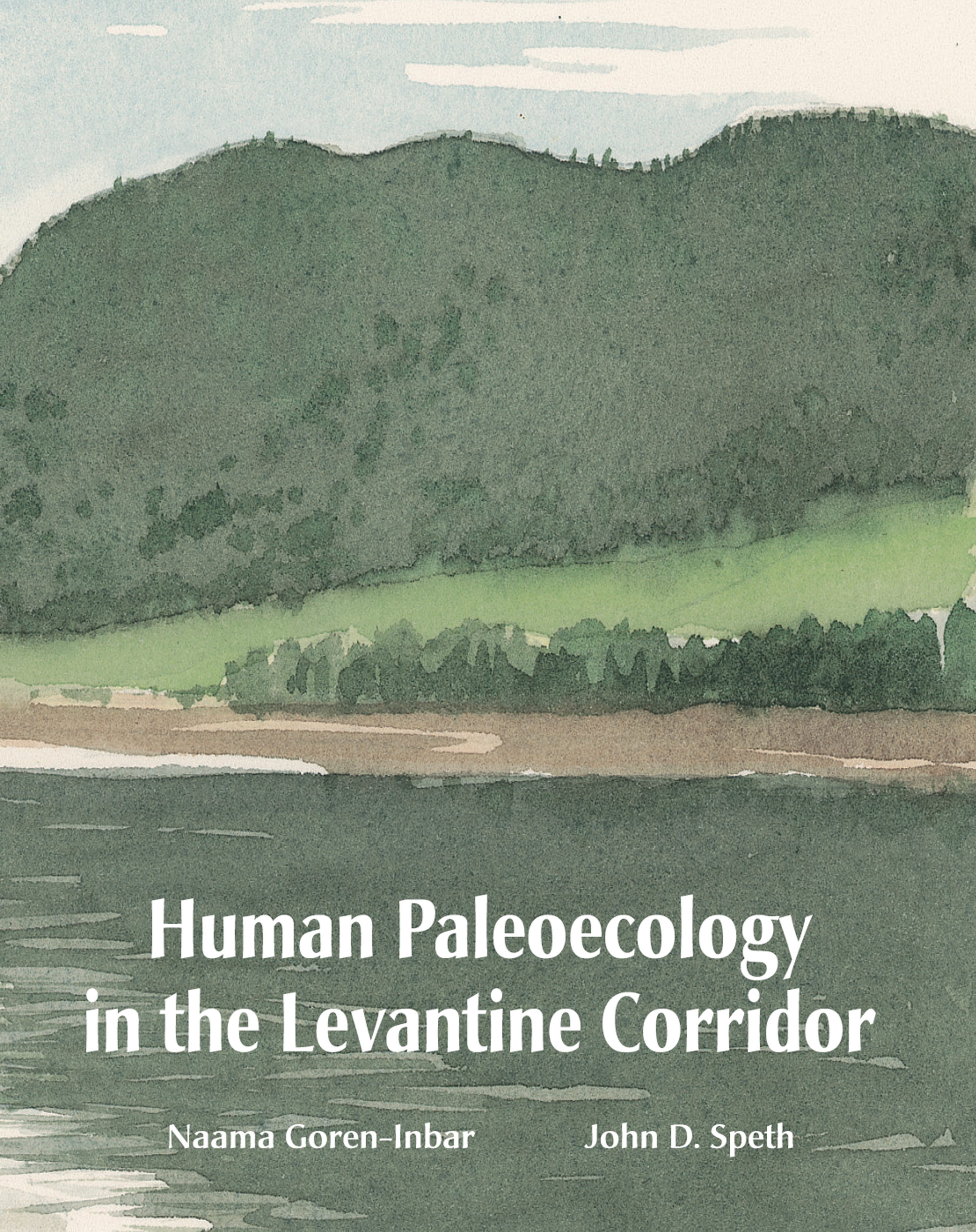

Human Paleoecology in the Levantine Corridor

Naama Goren-Inbar John D. Speth

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In memory of Eitan Tchernov, a prodigious scholar
who contributed enthusiastically, over many years
and in many and diverse biological disciplines, to
a better understanding of the “Levantine Corridor”

Table of Contents

Acknowledgments **vii**

List of Tables **xv**

List of Figures **xvi**

Introduction **1**
Naama Goren-Inbar and John D. Speth

Chapter I – The Levantine Waterway, Riparian Archaeology, Paleolimnology, and Conservation **5**
Dov F. Por
- Abstract 5
- Introduction 5
- Springs of Eden, rivers of Life 7
- Zoogeography of the western branch of the Aquatic Crescent 10
- Events coeval with Levantine humans 14
- Riparian cultures of the Levant 15
- Environmental challenges 17
- References 19

Chapter II – Quaternary Lake Margins of the Levant Rift Valley **21**
Craig S. Feibel
- Abstract 21
- Why lake margins? 21
- Implications 22
- Types of evidence 22
- The elephant site at Erq el-Ahmar 23
- The complex cycles of ʻUbeidiya 25
- Constrained cyclicity at Gesher Benot Ya'aqov 32
- Patterns of cyclicity in the Pleistocene lakes of the Levant 34
- References 35

Chapter III – Hippos, Pigs, Bovids, Saber-toothed Tigers, Monkeys, and Hominids: Dispersals through the Levantine Corridor during Late Pliocene and Early Pleistocene Times **37**
Bienvenido Martínez-Navarro
- Abstract 37
- Introduction 37

- Late Pliocene 37
- Early Pleistocene 40
- The significant taxa 42
  - *Pelorovis* 42
  - *Kolpochoerus* 42
  - *Hippopotamus* 43
  - *Megantereon whitei* 43
  - *Theropithecus oswaldi* 44
- Early Pleistocene Eurasian species in North Africa 44
- Discussion 44
- Conclusions 45
- References 46

Chapter IV – Ecological Interactions of Elephantids in Pleistocene Eurasia: *Palaeoloxodon* and *Mammuthus* 53
Adrian M. Lister
- Abstract 53
- Introduction 53
  - *Palaeoloxodon* 53
  - *Mammuthus* 55
- Ecological and evolutionary interaction between *Palaeoloxodon* and *Mammuthus* 56
- References 58

Chapter V – Long-term Continuity of a Freshwater Turtle (*Mauremys caspica rivulata*) Population in the Northern Jordan Valley and its Paleoenvironmental Implications 61
Gideon Hartman
- Abstract 61
- Introduction 61
- Shell morphology 62
  - *Significance of variation in shell morphology* 63
- *Mauremys caspica* at Gesher Benot Ya'aqov 64
- Genetic continuity of the Jordan Valley *Mauremys caspica* 65
  - Materials and methods 66
  - *Intraspecific variation in shell formulae in Trachemys scripta populations* 67
  - *Shell variations in recent populations of Mauremys* 68
  - *Shell anomaly in Mauremys caspica at Gesher Benot Ya'aqov* 69
- Discussion 69
  - *Mauremys caspica at Gesher Benot Ya'aqov* 69
  - *Differentiation of populations using shell anomalies* 70
  - *Shared shell anomaly and genetic continuity in fossil and present populations* 70
  - *Paleoenvironmental implications* 70
- Conclusions 72
- References 72

Chapter VI – Early Hominid Subsistence in the Levant: Taphonomic Studies of the Plio-Pleistocene 'Ubeidiya Formation (Israel) – Evidence from 'Ubeidiya Layer II-24 75
Sabine Gaudzinski
- Abstract 75

Introduction 75
The ʻUbeidiya Formation and its setting 75
Materials and methods 76
Layer II-24 of the ʻUbeidiya Formation 79
  The faunal assemblage 79
Summary and discussion 83
References 85

Chapter VII – Bands and Other Corporate Hominid Groups in Acheulian Culture 89
Emanuel Marx
Abstract 89
Introduction 89
The methodological problem 89
What are corporate groups? 91
Corporate groups in Acheulian culture 96
References 102

Chapter VIII – Culture and Genes in the Evolution of Human Language 105
Daniel Dor and Eva Jablonka
Abstract 105
Introduction 105
The evolution of language: The cultural engine 106
The genetic side of the coin: Partial genetic assimilation 109
Some theoretical issues 112
References 114

Chapter IX – Climate Variability in the Levant and Northeast Africa during the Late Quaternary Based on Marine and Land Records 117
Ahuva Almogi-Labin, Miryam Bar-Matthews and Avner Ayalon
Abstract 117
Introduction 117
Regional climatic settings 118
Paleoclimate proxies 119
Humid conditions during warm interglacial stages 120
Dry intervals during warm interglacial stages 124
Dry periods during cool glacial stages 126
Relatively humid periods during cool glacial stages 128
Summary 129
References 129

Chapter X – Dental Pathology, Stressful Events, and Disease in Levantine Early Anatomically Modern Humans: Evidence from Qafzeh 135
Anne-Marie Tillier, Henry Duday, Baruch Arensburg and Bernard Vandermeersch
Abstract 135
Introduction 135
Material 136
Aspects of the archaeological record 136
Dental health and oral hygiene in the Qafzeh hominids 137
  Periodontal diseases and antemortem tooth loss 138

        Evidence of tooth care or occupational modification? 139
        Search for carious lesions 139
    Indicators of non-specific stress and growth disturbances 139
        Developmental tooth enamel defects 139
        Infant mortality 140
    Soft tissue lesions and tumors of osseous origin 140
        Lesions of the ear 140
        Long bone lesions 142
    Cranial malformations 142
        Craniosynostosis 142
        Hydrocephalus 142
    Skeletal evidence of trauma 144
    Conclusions 144
    References 146

Chapter XI – Hunting Pressure, Subsistence Intensification, and Demographic Change in the Levantine Late Middle Paleolithic 149
John D. Speth
    Abstract 149
    Introduction 149
    Background and methods 150
    Average transport distance 153
    Seasonality 154
    Hunting pressure 157
    Conclusions 161
    References 162

Chapter XII – Wetland Drainage in the Levant (Lake Hula, Amik Gölü, and el-Azraq Oasis): Impact on Avian Fauna 167
Shoshana Ashkenazi
    Abstract 167
    Introduction 167
    The former large lakes of the Levant 170
        Lake Hula 170
        Amik Gölü 172
        El-Azraq Oasis 173
    The drainage stages and their consequences 174
    Complementary utilization of Levant wetlands by avian populations 175
        Lake Hula as wintering site for Amik Gölü breeding populations 175
        The Hula Nature Reserve as refuge for Amik Gölü avian populations 175
        Influx of wintering avian populations to northern Israel 176
        Changes in the Hula Nature Reserve breeding colony 177
        Inter-relations between avian populations of the Hula and el-Azraq wetlands 178
    Factors determining decline in waterbird populations 178
        Habitat loss 178
        Specimen collecting and hunting 179
        Pesticides and poisoning 179
        Weather conditions 180

Conservation implications 180
References 182
Appendix 185

Chapter XIII – "A Feather for Each Wind that Blows": Utilizing Avifauna in Assessing Changing Patterns in Paleoecology and Subsistence at Jordan Valley Archaeological Sites 191
Tal Simmons
Abstract 191
Introduction 191
Materials and methods 193
Seasonality 194
Climate and environment 198
Overarching trends and singular quirks 200
Discussion and conclusions 202
References 204

Chapter XIV – Natufian Behavior in the Hula Basin: The Question of Territoriality 207
François R. Valla
Abstract 207
Introduction 207
Territorial extension 209
Land use 212
The notion of ownership 213
Discussion 216
References 218

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List of Tables

Chapter III

Table 1. Large mammal faunal lists of the Early Pleistocene sites of Gesher Benot Ya'aqov, Israel; 'Ubeidiya, Israel; Dmanisi, Georgia; Venta Micena, Spain; and Ain Hanech, Algeria.

Chapter V

Table 1. Description of osseous shell anomalies and frequencies at which they appear in different populations of *Trachemys scripta* in North America.

Table 2. Definition and frequency of osseous shell anomalies in the present-day population of *Mauremys caspica* in the Jordan Valley.

Chapter VI

Table 1. Summary of analyzed faunal assemblages from sites of the 'Ubeidiya Formation.

Table 2. Size/weight classes for different taxa of the 'Ubeidiya Formation (after Bunn 1997).

Table 3. 'Ubeidiya layer II–24: taxa, NISP, and MNI.

Table 4. 'Ubeidiya layer II–24: skeletal element representation for size/weight class 2.

Table 5. 'Ubeidiya layer II–24: skeletal element representation for size/weight class 3.

Table 6. 'Ubeidiya layer II–24: skeletal element representation for size/weight class 4.

Table 7. Structural bone density of deer bones and % survivorship values for size/weight classes 2–4 in 'Ubeidiya layer II-24 by skeletal element and density scan site (after Lyman 1994: Table 7.6).

Table 8. Bone volume (cm^3; after Behrensmeyer 1975: Appendix 1) and size/weight classes 2 and 3 in 'Ubeidiya layer II-24 by skeletal element.

Chapter XI

Table 1. Crown-height values (mm) for lower (dP_4) and upper (dP^4) deciduous fourth premolars of gazelle and fallow deer.

Chapter XII

Table 1. Stages in the draining process of the large wetlands of the Levant.

Appendix. Avian species recorded in the former wetlands of the Levant.

Chapter XIII

Table 1. Cultural periods of Jordan Valley archaeological sites.

Table 2. Jordan Valley archeological sites indicating number of identified specimens (NISP) per site and number of identified avian taxa per site (N Taxa).

Table 3. The avifauna of Amud Cave.

List of Figures

Chapter I

Figure 1. A schematic map of the hydrographic network of the Levant.

Figure 2. Superposition of the distribution of the fish genus *Acanthobrama* and the "Levantine Corridor" *sensu* Bar-Yosef (1998).

Chapter II

Figure 1. Location map showing the major sites discussed in the text.

Figure 2. Graphic conventions used here to indicate shifting influence of lacustrine and sub-aerial conditions in the interpretation of cyclostratigraphic patterns.

Figure 3. Sketch stratigraphic section from the elephant site in the Erq el-Ahmar Formation, based on description and sampling undertaken in August, 1999.

Figure 4. Cyclostratigraphic interpretation of the sequence at the Erq el-Ahmar elephant site.

Figure 5. Stratigraphic sections of the 'Ubeidiya Formation, redrawn from Picard & Baida (1966) with additional short sections described and sampled in 1999.

Figure 6. Cyclostratigraphic interpretation of the first-order variability seen in the 'Ubeidiya Formation.

Figure 7. 'Ubeidiya Fi Cycle, showing interpreted environmental fluctuations based upon the Trench II record of Picard & Baida (1966).

Figure 8. Environmental fluctuations in 'Ubeidiya levels II-21 to II-26, as recorded in Profile 99-A, Trench IIb.

Figure 9. Environmental fluctuations in 'Ubeidiya levels III-21 to III-23, as recorded in Profile 99-B, Trench III.

Figure 10. Generalized cyclostratigraphic interpretation of environmental cycles at 'Ubeidiya.

Figure 11. Composite stratigraphic column from Gesher Benot Ya'aqov, with sedimentary cycles and major depositional environments indicated.

Figure 12. Cyclostratigraphic interpretation of the Gesher Benot Ya'aqov record.

Chapter III

Figure 1. Geographic situation of some of the most important Late Pliocene and Early Pleistocene localities of southern and western Asia, Europe and North Africa.

Figure 2. Biostratigraphic chart of selected Late Pliocene and Early Pleistocene large mammals in the Middle East and Europe.

Chapter IV

Figure 1. Known time-ranges of selected elephantid taxa in Eurasia: *Mammuthus meridionalis*, *M. trogontherii*, *Palaeoloxodon* spp.

Chapter V

Figure 1. *Mauremys caspica* shell diagram.

Figure 2. Comparison between recent and fossil bony plate shell elements of *Mauremys caspica* turtles from the upper Jordan Valley of Israel.

Figure 3. Common bony plate anomalies in *Mauremys caspica* shells from the present-day population of the upper Jordan Valley.

Figure 4. The anomalous longitudinal split of neural 8 in a fossil specimen from GBY.

Chapter VI

Figure 1. 'Ubeidiya layer II-24, differing stages of bone preservation demonstrated for Phalanx 2 of Cervidae gen. et sp. indet.

Figure 2. 'Ubeidiya layer II-24, *Hippopotamus behemoth* metatarsus and pelvis from neonatal individuals.

Figure 3. 'Ubeidiya layer II-24, fragment of 2nd cervical vertebra of size/weight class 3 animal with cut-marks on cranial/ventral rim (cut-marks shown at 3x magnification).

Chapter IX

Figure 1. Location map showing the six sites in the SE Mediterranean Sea, the Levant, the Red Sea, and the Gulf of Aden from which the records were taken for the paleoclimate synthesis.

Figure 2. Comparison between the $\delta^{18}O$ record of *Globigerinoides ruber* from core MD 84 641 (modified after Fontugne & Calvert 1992) and the oxygen isotope record of Soreq Cave speleothems for the time period of 185 Ka to the present day and Peqiin Cave speleothems from 250 to 185 Ka.

Figure 3. $^{87}Sr/^{86}Sr$ ratios of Soreq Cave speleothems (black squares) superimposed on $\delta^{18}O$ profile against age for the last 60 Ka (from Ayalon et al. 1999). The high $^{87}Sr/^{86}Sr$ values reflect exogenic sources (dust and marine spray); the lower values are closer to the Upper Cretaceous dolomitic host rock value of 0.7074.

Figure 4. The $\delta^{18}O$ record of *Globigerinoides ruber* (a) of core M5/2-174/87-2, KL 11 (Hemleben et al. 1996), central Red Sea, during the last 380 Ka. Numbers on the right side of the stable isotope record indicate marine isotope stages (MIS) and substages, and the relative abundance of epipelagic (b) pteropods (modified after Almogi-Labin et al. 1998). The vertical dashed line indicates the % epipelagic pteropods at present. Solid arrows represent periods with more humid conditions during interglacial intervals and open arrows indicate periods of more humid conditions during glacial stages. The shaded areas indicate glacial intervals.

Figure 5. The relative abundance of *Limacina bulimoides*, a mesopelagic pteropod, out of the total pteropods during the late Holocene, from three multicores from the central Red Sea: MC98, 579 m water depth; MC93, 929 m water depth; and MC91, 1781 m water depth plotted against uncalibrated ^{14}C age (modified after Edelman-Furstenberg 1998).

Figure 6. The $\delta^{18}O$ record of *Globigerinoides ruber* (a) of core M5/2-174/87-2, KL 11, central Red Sea, during the last 380 Ka (Hemleben et al. 1996). Numbers on the right side of the stable isotope record indicate marine isotope stages (MIS) and the relative abundance of the mesopelagic pteropod *Limacina bulimoides* (b) out of the total pteropods (modified after Almogi-Labin et al. 1998). The shaded areas indicate glacial intervals.

Figure 7. The $\delta^{18}O$ record of *Globigerinoides ruber* of core M5/2-174/87-2, KL 11 (open circles), central Red Sea (Hemleben et al. 1996), superimposed on the $\delta^{18}O$ values of *G. ruber* of core M5/2-259/87-2, KL15 (solid circles), Gulf of Aden (Almogi-Labin et al. 2000), showing similarity between the isotopic trends. Numbers on the right side of the oxygen isotope record indicate marine isotope stages (MIS). The shaded areas indicate glacial intervals.

Chapter X

Figure 1. Aspects of oral health in the Qafzeh hominids.

Figure 2. Soft-tissue lesions and tumor of osseous origin.

Figure 3. Cranial malformation and trauma.

Chapter XI

Figure 1. Location of Kebara Cave in the Southern Levant.

Figure 2. Proportion of gazelle and fallow deer among the larger mammals at Kebara Cave (%NISP, calculated on the basis of NISP values for 7 taxa – *Bos*, *Capra*, *Cervus*, *Dama*, total equids, *Gazella*, and *Sus*; total NISP=14,962).

Figure 3. Relative skeletal completeness of gazelle and fallow deer as approximated by the ratio of $\sum$NISP/MNI.

Figure 4. Crown-height measurements (mm) for lower third molars (M_3) of gazelle.

Figure 5. Crown-height measurements (mm) for lower third molars (M_3) of fallow deer.
Figure 6. Crown-height measurements (mm) for deciduous lower fourth premolars (dP_4) of gazelle (NISP=107).
Figure 7. Smoothed oxygen-isotope record ($\delta^{18}O$ ‰ PDB), derived from speleothems in Soreq Cave (Israel), for the period 60,000–45,000 years ago. Original data provided by M. Bar-Matthews (see Bar-Matthews et al. 1999:88, their Figure 1A for unsmoothed record).
Figure 8. Proportion of juvenile gazelle (%NISP) at Kebara, based on the frequency of unfused and fusing epiphyses.
Figure 9. Mean crown height values of *adult* deer (NISP=191) and gazelle (NISP=404) lower third molars (M_3) plotted by arbitrary one-meter-thick levels.

Chapter XII

Figure 1. Regional map of the former large wetlands of the Levant. Stars denote the main wetlands mentioned in the text (base map drawn by Eitan Tchernov).
Figure 2. Trends in winter counts of selected waterbird populations in Israel. Based on Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980.
Figure 3. Trends in wintering populations of selected waterbirds in Israel. Based on Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980.
Figure 4. Changes in species composition of the Hula Nature Reserve breeding colony. Based on Suaretz & Paz (1975) and Ashkenazi & Yom-Tov (1997).

Chapter XIII

Figure 1. Location of Jordan Valley archaeological sites.
Figure 2. Seasonal presence of birds at 'Ubeidiya and Gesher Benot Ya'aqov.
Figure 3. Seasonal presence of birds at Ohalo II.
Figure 4. Seasonal presence of birds in the Natufian.
Figure 5. Representation of the seasonal presence of birds in the PPNA (Netiv Hagdud depicted here).
Figure 6. Seasonal presence of birds in the Late PPNB levels of Bawwab al-Ghazal.
Figure 7. Preferred avian habitats at 'Ubeidiya and Gesher Benot Ya'aqov.
Figure 8. Preferred avian habitats at Ohalo II.
Figure 9. Preferred avian habitats in the Natufian.
Figure 10. Preferred avian habitats in the PPNA.
Figure 11. Relative frequencies of avian Families on archaeological sites over time.

Chapter XIV

Figure 1. Basalt sources used for tools at Hayonim Cave, el-Wad, and Eynan (after Weinstein-Evron et al. 2001).
Figure 2. Flint sources used by Early Natufian people from Hayonim Cave and Eynan (after Delage 2001).
Figure 3. Detail of grave H. 104 at Eynan showing the hand of a woman on the body of a puppy (photo by F. Valla and A. Dagand).
Figure 4. Detail of grave H. 7-8-10 at Hayonim Terrace: note the dog's hind leg on the skull of H. 10 (Photo by F. Valla).

Introduction

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While the earliest hominins originated in Africa, at some time after about 1.8 Ma an archaic species of human – *Homo ergaster* – expanded out of Africa, very likely first occupying the Levantine Corridor before spreading into Eurasia. Scholars of diverse disciplines now believe that anatomically modern *Homo sapiens* also originated in Africa and again expanded into the Levantine Corridor before spreading into Europe and the rest of Asia. While the behavior of hominids in Africa and its paleoecological context have for many years been the focus of intensive interdisciplinary research, a comparably in-depth interdisciplinary look at evolving human adaptations and paleoecology within the Levantine Corridor has never been undertaken. It is clear that this Corridor has repeatedly played a pivotal role in the course of human evolution, witnessing both migration and adaptation as successive waves of human ancestors moved out of Africa. In order to understand the nature of these migrations, and to better understand how humans were able to adapt to social, demographic, and environmental conditions very different from those in which they had evolved, it is critical that the human paleoecology of the Levantine Corridor be subject to the kind of in-depth interdisciplinary scrutiny that has proved so fruitful in Africa.

The archaeological record of the Levantine Corridor is unique, as some of the world's most significant Paleolithic, Epipaleolithic, and Neolithic developments can be documented there. These range between the earliest, 'Ubeidiya (1.4 Ma) and Gesher Benot Ya'aqov (0.78 Ma), both bearing African affinities but distinctly different from each other; deeply stratified Middle Paleolithic cave sites, such as Tabun, Skhul, Qafzeh, Hayonim, Amud, and Kebara, that were occupied by Neanderthals and the earliest anatomically modern humans outside of Africa (ca. 250–45 Ka); the Kebaran site of Ohalo II, with the oldest huts in the Levant (23 Ka); and the world's first sedentary or nearly sedentary communities, such as the superbly preserved Natufian village of Eynan (ca. 12 Ka), where the stage was set for the development of agriculture, the most dramatic transformation in the human career.

Despite the one-and-a-half-million-year-long record of human migration, adaptation, and evolution within the Levantine Corridor, there has never been a serious multidisciplinary effort to integrate the separate threads of information within a more general framework of human paleoecology. To initiate such an integration, a group of internationally recognized experts from Israel, France, Germany, Spain, Denmark, and the USA gathered in Jerusalem at the Institute for Advanced Studies (IAS) of the Hebrew University to address a range of interrelated topics, which together form the core of this enterprise. Some experts were specialists in the archaeology of the region, while others had the expertise needed to integrate the prehistoric record within a broader paleoenvironmental and ecological perspective. Among these were experts in paleontology, biogeography, the structure and composition of Mediterranean ecosystems, the economic and social formations of foragers and pastoralists, and various other facets. Over a period of six months (March–August 2002), and through a combination of individual research, weekly seminars, several workshops and guided field excursions, and a public conference held in mid-July 2002, participants exchanged ideas and forged new interdisciplinary research endeavors. This book represents the first major product of the collaborative interaction that was initiated through the IAS-sponsored project. We anticipate that this is just the beginning of what will prove to be a long-lasting and productive phase of integrative research on the "Human Paleoecology in the Levantine Corridor."

Scholars can conceive of the "Levantine Corridor" in a variety of different ways, from a very narrow or minimalist definition that incorporates only the Rift Valley itself to a broader, more inclusive view (the one we use here) that sees the Corridor as encompassing the entire strip of land – rift, uplands, and coastal zone – bounded by deserts on the east and the Mediterranean Sea on the west. The Levantine Corridor, throughout the period that humans have been present there, has been an area of great biodiversity, providing a wealth of aquatic and terrestrial resources that have been vital to the success of human adaptations in the region. But the area has also been an incredibly dynamic one, affected both by global changes in climate over the course of the Pleistocene and by local tectonic and volcanic instability in the rift system itself. The papers in this volume explore this diversity and dynamic history in a number of distinct though complementary ways, which in their totality provide a vital framework for understanding changing human adaptations and evolution in the Near East.

We begin the volume with a chapter by Por (I) that explores the nature, history, and extraordinary resource potential of the springs, rivers, and lakes that developed in and adjacent to the Levantine Rift Valley. These waterways are unquestionably one the most striking and important features of the Levantine Corridor, and provided an absolutely vital and highly diverse resource base for humans ever since the earliest expansion of our ancestors out of Africa.

Next, in the chapter by Feibel (II), we focus our lens much more tightly, both spatially and temporally, and take a detailed look at the geology and paleoenvironments revealed by the deposits at two of the most important Lower Paleolithic archaeological localities in the Levantine Corridor – 'Ubeidiya (Early Pleistocene) and Gesher Benot Ya'aqov (Early–Middle Pleistocene). The sequences at both sites reveal a complex record of multiple human occupations along the fluctuating margin of ancient lakes.

Martínez-Navarro, in the next chapter (III), explores the unique role of the Levantine Corridor as an extension of the East African rift system, and as an intercontinental bottleneck in the dispersal of animals, and perhaps humans, from Africa via the Levant into Eurasia. Particularly interesting is the discovery of several evolved African taxa in the Early Pleistocene of Eurasia, including the primate *Theropithecus oswaldi*, a saber-toothed tiger, *Megantereon whitei*, and several ungulates. Martinez-Navarro explores the implications of these African immigrants for understanding the early expansion of the genus *Homo* into the Levant and beyond.

Also looking at faunal evidence from the Near East, Africa, and Eurasia, but this time focusing specifically on elephants, Lister (Chapter IV) provides a detailed account of the spread of straight-tusked elephants of the genus *Palaeoloxodon* into the Levant and Eurasia from Africa in the time period of roughly 800–600 Ka. During this interval *Mammuthus meridionalis* (ancestral mammoth) became extinct, perhaps triggered by the arrival of *P. antiquus,* competing for its woodland habitat.

Hartman (Chapter V) continues in the faunal vein, focusing on freshwater turtles of the species *Mauremys caspica* recovered from the important Acheulian site of Gesher Benot Ya'aqov. Because of a distinct bony-plate shell anomaly that is shared by both fossil and present-day Jordan Valley populations of *M. caspica*, but that is unknown in northern populations of the same species, he concludes that there has been genetic continuity between the ancient and modern animals. The continuous existence of this turtle population within the Levantine Corridor since at least the early Middle Pleistocene argues for a surprising degree of environmental stability despite repeated tectonic activity, volcanism, and climatic oscillations.

Gaudzinski (Chapter VI) also looks at Early Pleistocene animals, in this case specifically those from ʻUbeidiya, but now the focus shifts from reconstructions of paleoenvironments and patterns of species dispersal to the issue of whether the bones found along the margins of the ancient lake are part of the natural background or instead are food remains of the hominids who frequented the water's edge. The presence of cutmarks on a number of the bones clearly shows that humans played a role in the formation of the bone assemblages. Interestingly, however, Gaudzinski finds no evidence that the bones had been broken open for their marrow content, a pattern that typifies most Paleolithic faunal assemblages. Though tentative, Gaudzinski's study raises the possibility that the ʻUbeidiya hominids hunted some of the animals found there, particularly the medium-sized ones.

Chapter VII, by Marx, departs from the empirical focus of the previous chapters and attempts instead a reconstruction of the likely form of human social organization in the Acheulian. Marx suggests that one-to-one, or dyadic, relationships for companionship, sexual relations, and reproduction, and egalitarian task-oriented, or corporate, groups for food-gathering, hunting, and tool-making, were the principal forms of collaboration among Acheulians. Long-lasting domestic groups (families), kinship ties beyond the links between mother and child and among siblings, and territorial entities such as the "tribe" probably did not yet exist.

After the exploration of the nature of human societal form in the Lower Paleolithic in the previous chapter, the next one by Dor and Jablonka (VIII) develops an interesting theoretical model for the development of human language in which genetic evolution is thought to follow, rather than precede, cultural evolution. In their model, the process begins with the cultural evolution of linguistic communication, which then gradually unmasks genetic variations within hominid populations, ending up with partial genetic assimilation of a variety of learning capacities, some of which are linguistic. As this process of cultural-genetic co-evolution continues, it can lead to increasing sophistication of the linguistic system, culminating in the establishment of language as a major system of social interaction.

In the next chapter (IX), Almogi-Labin, Bar-Matthews, and Ayalon return to the issue of paleoclimates in the Levantine Corridor, but this time with the focus on the last 400,000 years of the Pleistocene. The authors combine well-dated marine isotopic records from the Mediterranean Sea, Red Sea, and Gulf of Aden with isotopic records from cave deposits (speleothems) in Israel. The combined records, which span several complete glacial-interglacial cycles, provide archaeologists, paleontologists, biogeographers, and others with an invaluable and highly detailed record of the paleoclimatic history of the Near East.

Chapter X, by Tillier, Duday, Arensburg, and Vandermeersch, moves us into the last 100,000 years of the Pleistocene and into the archaeological period known as the Middle Paleolithic. The unusual cluster of burials of "anatomically modern humans" from Qafzeh Cave (Israel), the majority of which failed to attain reproductive adulthood, provides unique insights into childhood health, nutrition, and aspects of social organization. Their studies of the teeth of these burials reveal little evidence of physiological stress. The skeletal remains also show few signs of trauma and injuries. Several of the children, however, suffered from infection and significant pathologies. Nevertheless, life in the Middle Paleolithic was not as "brutish" as many have envisioned it; the burials reveal surprising evidence of special care given to unhealthy individuals that was maintained until their death, and in at least one case the deceased adolescent was placed in the ground accompanied by grave goods.

The next chapter (XI), by Speth, continues the focus on the Middle Paleolithic, but turns to the hunting behavior of "anatomically pre-modern humans" – the Neanderthals – as revealed by animal bones from the 60–40 Ka levels in Kebara Cave (Israel). This paper develops the hypothesis that the size of the Neanderthal population utilizing Kebara by the late Middle Paleolithic may have grown to a level sufficient to exert pressure on local populations of larger animals like aurochs and red deer, compelling hunters to greater use of juvenile and young adult gazelle, a trend of subsistence-related intensification that continued unabated into the early Upper Paleolithic. If future work reveals a similar trend elsewhere in the Levantine Corridor, it would indicate a major region-wide human demographic upswing sometime after 60–55 Ka.

Ashkenazi, in the next chapter (XII), again looks at the wetlands in the Levantine Corridor, focusing specifically on the diverse populations of birds that until recently utilized the region's major water bodies – Lake Hula (Israel), Amik Gölü or Lake Antioch (Turkey), and el-Azraq Oasis (Jordan). Ashkenazi's contribution documents the negative impact of recent drainage on the avifauna that once utilized these wetlands, showing in the process that changes affecting any one of the water bodies would have significant consequences for the bird populations utilizing the others. The author concludes with specific suggestions for rehabilitating these wetlands. Ashkenazi's chapter provides a valuable backdrop for the next contribution, which looks at the use of birds for food and other purposes by Pleistocene and more recent human populations in the Levantine Corridor.

Birds have been recovered from Pleistocene and more recent archaeological sites throughout the Levantine Corridor. Their study by Simmons (Chapter XIII) provides insights into changing paleoenvironmental conditions in the Jordan Valley from Early Pleistocene times up to approximately 7,000 years ago. The avifauna also shed light on the seasonality and degree of sedentism of these prehistoric occupations, the microhabitats that their inhabitants exploited, and human subsistence preferences. Simmons shows that the prevailing pattern of bird exploitation throughout prehistory relied first and foremost on waterfowl that wintered in the wetlands, supplemented by birds that came into the area with the autumn and spring migrations; birds that frequented shoreline, grassland, and woodland habitats were always much less important.

In the last chapter, Valla (XIV) considers evidence from the Natufian site of Eynan (Mallaha) in the Hula Basin to determine whether these Epipaleolithic foragers, on the threshold of sedentary village life, were territorial in their relationship to land, resources, and neighboring Natufian groups. He finds little convincing evidence of territoriality or population packing in the Natufian record and, on the basis of these insights, hypothesizes that models for the origins of agriculture that envision population pressure as the primary force that propelled human groups toward cultivation and plant domestication need to be reconsidered.

The comprehensive study of "Human Paleoecology in the Levantine Corridor" is a challenging and multi-faceted research endeavor that integrates insights from a wide spectrum of disciplines and approaches. The research that grew out of the IAS-sponsored project held at the Hebrew University in 2002, and that is reflected in the contributions in this volume, marks a productive and rewarding step in that direction, one that we hope will be followed soon by additional steps toward the same ultimate goal. This is an exciting time in the study of human evolution, and the unparalleled record of evolving human lifeways and adaptations in the Levantine Corridor holds the key to deciphering some of the most important chapters in the human story.

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Chapter I

The Levantine Waterway, Riparian Archaeology, Paleolimnology, and Conservation

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Abstract

The Levantine aquatic corridor is the product of the ongoing rifting process in the Middle East. A "stepping-stone" chain of longitudinal river basins in the basically arid Levant probably served as a precondition for human expansion out of Africa. It has likely been a duplication of the expansion of the aquatic biota in these freshwater enclaves. Tectonics, volcanism, and paleolimnologic events were coeval with the different waves of Levantine settlers. Attention is given to the lakes and rivers, but first of all to the chain of strong artesian springs which functioned permanently despite fluctuating Pleistocene climatic conditions. The sequence of the Jordan-Litani-Orontes Basins is fed and maintained by such springs. The very narrow and discontinuous Mediterranean coastal plain, especially north of Haifa, could not serve as an alternative route. The role of spring-fed marshlands is especially evident in the case of the riparian Natufian settlements and the early stages of cultivation. Preservation and restoration of such sites that are not yet disturbed is urgently needed for documentation and research of both biodiversity and archaeology.

Introduction

The purpose of this paper is to shed light on the importance of the limnological environmental setting for human prehistory in the Levant. The importance of riparian sites in the Levantine Corridor, the western branch of the Fertile Crescent, for human expansion out of the African cradle became obvious with the discovery in the 1960's of the Late Pliocene site of Erq el-Ahmar (Stekelis 1960; Tchernov 1975) and the Early Pleistocene localities at 'Ubeidiya on the Jordan River (Bar-Yosef & Tchernov 1972). There are many other sites, including more modern ones, which underscore the importance of the Dead Sea and Syrian rift valleys in this corridor. Throughout the Pleistocene, the corridor provided propitious conditions for multiple northbound waves of human migration. Epipaleolithic and early Neolithic sites in the Jordan Valley have also shown that very important steps of the transition to sedentary life and to cultivation occurred there. Rather than being merely a connecting passageway, the Levantine Corridor provided a sustained set of suitable habitats for the autochthonous biological and cultural evolution of the waves of African expatriates. Although the majority of known archaeological sites, both Pleistocene and later, are concentrated in the Jordan section of the rift valley, where investigations have taken place since those of Picard (1960) and Perrot (1966), the following discussion will attempt to deal with its entirety.

In the literature, the uplifted parallel Cis- and Trans-rift mountain chains are seen as the principal factor for the southward extension of Mediterranean climate into the Syrian desert (Por 1975). Contained between the two chains, the rift valley itself, at least in its southern part, is known to be the northward extension of tropical "Sudanese" climate, with tropical biota similar to those of the African hominid savanna homeland.

The role of spring-fed oases, rivers, and river-fed water bodies in the graben, which are largely a product of tectonics, has not been sufficiently emphasized (Por 1975; Por & Dimentman 1989). These oases are the "stepping-stones" in a sequence of rivers.

The *exorheic* (i.e., rivers emptying in the sea) Nile and Euphrates River Basins experienced a very tumultuous hydrographic history related to sea-level fluctuations during the Pleistocene. Consider, for example, the catastrophic rapidity with which the area of the Persian Gulf was reinvaded by the sea during the post-glacial Flandrian transgression, modifying the hydrographic baseline of the Euphrates. The hydrographic story of the Nile and its delta has been even more unstable, as this river often turned into a huge seasonal stream. While both river systems cross and fertilize major desert regions, they are fed by distant headwaters situated in regions with much higher precipitation. For the hydrographer, these rivers are *xenorheic*, i.e., "foreign rivers," in their lower desertic reaches.

In contrast, the much more modest river basins of the Levantine rift valley were largely isolated from the Mediterranean after the termination of the Pliocene marine gulf and the uplifting of the Cis-rift mountain ranges. Since that date, the water bodies of the rift have had a prevalent tendency to be *endorheic*, i.e., to end up in terminal lakes or in terminal swamps and *sabkhas* (salt pans) rather than emptying into the sea. Outflow to the Mediterranean was episodic. World sea-level changes did not influence these rivers, which are fed by autochthonous abundant and stable springs (karstic exsurgent outpours) that render them independent of the drainage of the surrounding intermittent mountain torrents and wadis. These are artesian springs that drain ancient aquifers rather than collecting surface runoff. The output of these springs, therefore, shows little variation in response to secular climatic fluctuations. During the Pleistocene of the Levant, ongoing tectonic faulting repeatedly created new or rejuvenated *endorheic* river basins.

This is a rather unique hydrographic situation, since most rivers of the world are fed by intricate confluent headwaters that start in surface springs situated at high elevations. The output of these springs depends on rainwater runoff or on shallow recent water tables. In the semi-arid climate of the Middle East, the surface springs dry out during the summer or during years of drought and the streams turn into empty wadi beds. If the rivers end up in terminal lakes, these lakes tend either to turn into saline *sabkhas* or to dry out completely in response to changing pluvial regimes. Quite significantly, the Hebrew name for such ephemeral streams is "*nahalei achzav*", i.e., "disappointing streams," whereas the perennial artesian-fed streams are called "*nahalei eitan*," i.e., strong, reliable ones.

Because of this general background of hydrographic homeostasis, a permanent chain of rivers and wetlands was always present during the Pleistocene of the Levant, despite fluctuating sea levels and changing pluvial regimes. This longitudinal chain of oases provided for the existence of a rich variety of ecological resources in the rift valley that might have been particularly attractive to the hominids of the Jordan-Dead Sea rift during Pleistocene times (Werker & Goren-Inbar 2001). Along this western branch of the Fertile Crescent, by taking advantage of the wetlands humans could have expanded in subsequent waves, little influenced by the climatic hardships of the neighboring Syrian desert. Throughout the Pleistocene, the Levantine Corridor experienced a milder microclimate, produced by the lakes and rivers in the rift valley with their local evaporation-precipitation regime.

Because of its lakes and oases, the Levant became the most important passageway for European bird migration to and from Africa. This provided an additional resource for the hunters and trappers of the rift valley. Paradoxically, the crisis times of the full Glacials in Europe, with increased bird migration, were probably years of bounty for the hunters and trap-setters of the Levant Corridor.

The Levantine coastal plain, supplied with sediment from the Nile, is relatively broad in the south, but gets narrower and narrower and practically ceases to exist north of the Gulf of Haifa. There is no "*Via Maris*" along the Lebanese and Syrian coasts, since the Lebanon and Ansariya Mountains drop off abruptly into the sea. Isolated pockets of lowlands exist only at the mouths of the mountain streams. Nor were broad coastal plains exposed by lowered sea level during Glacial periods, since deep and steep submarine canyons accompany the shore from the western Galilee northward. In addition, as mentioned by Bar-Yosef (1998), the poor and unproductive eastern Mediterranean could not supply sufficient marine foods for large human settlements. There are no kitchen middens on our shores. Like so many armies in the millennia to follow, upon reaching the Carmel promontory, the wave of human settlements had to move inland along the rivers and lakes of the rift valley.

Springs of Eden, rivers of Life

The idea of Paradise has always been associated by the ancient people of the arid Middle East with life-giving springs and rivers. Sura 55 of the Quran identifies Eden as a place with "two springs pouring forth water in continuous abundance." The biblical Paradise is a place from which four rivers flow out. In the widespread tradition these rivers are the Euphrates, the Tigris, and the unidentified Gihon and Pishon. More precisely, the Arab popular tradition associates Paradise with the rich artesian spring of the Barada River near the foothills of Mount Hermon and with the oasis of el-Ghutta, near Damascus, which is fed by this *endorheic* river. In more concrete, but still poetic terms, the massif of Mount Hermon, "Jebel esh-Sheikh," is also called "the Father of the Rivers." At 2,814 m, it is the highest peak in the region and forms the abruptly ending southern extension of the Anti-Lebanon Range. Unlike its surroundings, the Hermon is built of uplifted Jurassic limestone, a porous karst formation rich in fissures and crevices. Snow-covered for a good part of the year, this mountain was possibly an isolated southernmost point where ephemeral Pleistocene glaciers could develop. Efficiently blocked towards the south by the Golan basalt fields, the Hermon has very little surface runoff and almost all the snow feeds deep karstic aquifers that emerge in the adjacent synclines in the shape of several strong exsurgent vauclusian rivers.

We are dealing with fossil aquifers that accumulated during the last pluvial episodes (Geyh 1994). The headwaters of four main rivers, the Jordan (formed by its three confluent headwaters), the Litani, the Orontes, and the Barada, emerge from the Hermon aquifer in a very small and privileged piedmont area of only about 2,000 square kilometers (Figure 1). Less impressive, the Awaj River, which also flows eastward into the Syrian desert, south of the Barada, can also be added to this list. The existence of the Levantine waterway, formed by the rivers of the rift valley, depends on the headwater springs of the Hermon aquifer. Without the uplifted Jurassic peaks of the Hermon, the Levantine waterway would probably not exist. Though essentially true, this is a somewhat oversimplified statement, since many more and smaller artesian springs emerge along the rift valley itself, especially along the Orontes, and there is also a not negligible input of rainwater. It has been calculated that the Hermon aquifer supplies a total annual volume of around 800 million cubic meters. This represents the environmental baseline of the Levantine Corridor and, for the desert people, the nearest approximation to the idea of Paradise. Neither in the present nor in past arid episodes is it likely that the permanent base flow of these rivers could have been sustained by rainwater runoff from the desert wadis alone. By a rough average estimate, the deep aquifers supply about 50% of the total flow of the main rivers of the Levant. This is enough to maintain a constant flow in these rivers, even during periods of excessive aridity.

Among the rivers of the Levantine Corridor, the hydrology of the Jordan River is the best known. This river results from the union of three headwater streams, all emerging as strong springs fed in different proportions by the Hermon aquifer. First among them, the stream of Nahal Dan is by far the most abundant and stable source. It is a full-fledged river that gushes out from its subterranean course. The Dan alone supplies 50% of the total flow of the upper Jordan. The output of Nahal Dan shows little seasonal fluctuation and little rainfall influence, since it is in fact an emergent subterranean river. Its average annual discharge is an impressive 245 million cubic meters and the multi-annual variation over a twenty-year period was only between a baseline flow of 173 and a maximal flow of

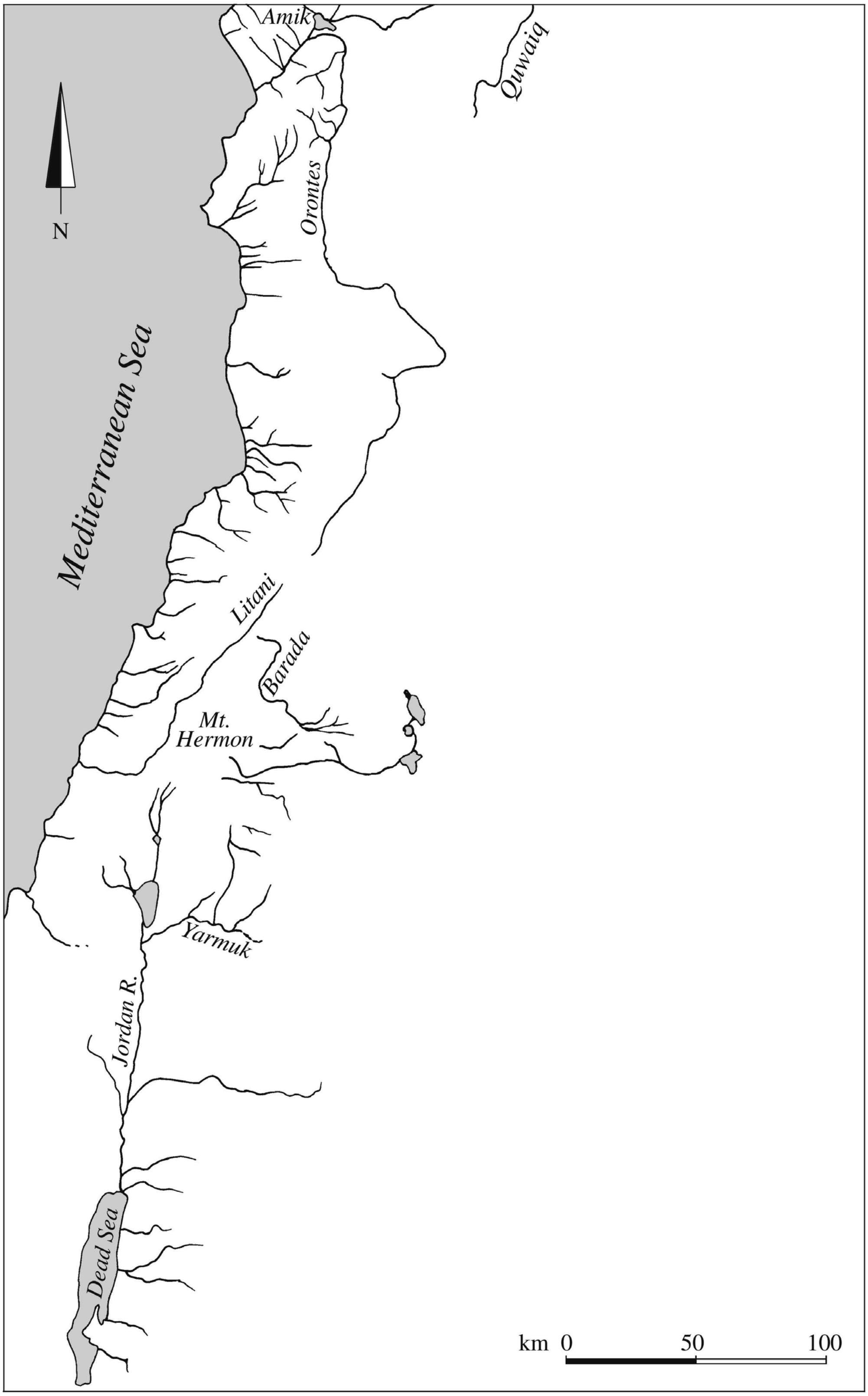
Amik
Quwaiq
N
Orontes
Mediterranean Sea
Litani
Barada
Mt. Hermon
Yarmuk
Jordan R.
Dead Sea
km 0 50 100

Figure 1. A schematic map of the hydrographic network of the Levant.

285 million cubic meters. Even today, this discharge can supply more than one-tenth of the water needs of modern Israel. The world-famous exsurgence of Vaucluse in southern France, already known as a natural phenomenon in classical antiquity, has given its name to this whole category of karstic springs. Its discharge is less than twice the volume of the Dan.

The Banias, or Nahal Hermon, the second headwater stream of the Jordan, with a medium discharge of 121 million cubic meters, exhibits a multi-annual variation of between 63 and 190 million cubic meters. Finally, the third headwater, the Hasbani, is a river in its own right, as it runs independently for some 50 km before joining the other two source streams of the Jordan. The Hasbani is formed by two artesian springs, the Hasbayyaa and the Wazzani, but on the way collects considerable runoff. With an average yearly output of 138 million cubic meters, its flow varies between a baseline of 52 million cubic meters and a maximum of 236 million cubic meters. The greater variability reflects its increased dependence on fluctuations in regional rainfall over the years.

The united upper Jordan then enters the valley of Lake Hula and its swamps. Before being drained in 1958, the lake occupied some 12–14 square kilometers. The area of the surrounding swamps fluctuated seasonally between 10 and 50 square kilometers. This lake received input from a number of springs, among them the very abundant karstic spring of 'Eynan ('Ein Mallaha), with a medium discharge of 20 million cubic meters per year, and with very little seasonal and multi-annual fluctuation. Before being captured for irrigation, it fed a small 3-km-long tributary river (Dimentman et al. 1992). The middle Jordan then descends rapidly through the gorge of Benot Ya'aqov to reach Lake Kinneret, which is already around 200 m below sea level. The basin of the lake is situated in that segment of the rift valley that was invaded by the Pliocene Mediterranean. Consequently, this segment of the valley still receives springs that drain old saline aquifers. As many, or even most, of the springs that flow into the lake are salty, Lake Kinneret is slightly oligohaline, at the limit of brackish waters. It therefore makes, at best, very poor drinking water. Most important is the spring complex of Tabgha, the classical Heptapegon, which supplies the Kinneret with a fairly stable yearly average output of 20 million cubic meters of a mixture of fresh and salty waters. Another abundant salt-water spring, Maayan Habarbutim, is sub-lacustrine.

As the lower Jordan leaves Lake Kinneret, descending on its meandering course to the Dead Sea, which at present is 417 m below ocean level, it still receives one important freshwater tributary. This is the Yarmuk River, which once contributed a yearly average of 94 million cubic meters to the Jordan. This amounts to almost the other 50% of the water carried by the lower Jordan. The Yarmuk takes its origins from the artesian Muzayrib spring and other smaller springs. It is commonly assumed that the Yarmuk is also fed by the Hermon aquifer, surfacing far to the south, where the cover of the Golan basalt exposes underlying Jurassic rocks. However, the Yarmuk is fed mainly by runoff, since it has a baseline flow of only 13 million cubic meters in the late summer month of September, as compared with 100 million in the rainy month of February.

Farther down the valley, the Jordan and the Dead Sea receive fresh water from the artesian spring of 'Ein el-Sultan near the site of Jericho and the oasis springs of Ghor es-Safi in the far southeastern corner of the Dead Sea. The Mujib (Arnon) River and the small mountain stream of Wadi Kelt are perennial watercourses. There are several salty springs, like 'Ein Feshkha, a non-potable oligohaline spring and oasis near the site of Qumran and, on the opposite shore of the Dead Sea, the hot and saline stream of Zarqat Main, the classical Kallirrhoe. But more than anything else, the level of the Dead Sea depends on the inflow of the Jordan and the amount of runoff reaching it from the two bordering mountain escarpments. In addition, torrents coming from the Judean Desert might have been permanent rivers during periods of wetter climate. The ionic composition of the very concentrated brine of the practically lifeless Dead Sea represents in an amplified concentration the ionic relations of the distant Tabgha springs on the shore of Lake Kinneret.

On the eastern slope of Mount Hermon the Barada River, in association with the smaller Awaj River, waters the large oasis of Damascus in Syria. The main source of the Barada is the strong artesian spring of 'Ein Fidje with a current output of some 70 million cubic meters per year. This estimate, however, represents the present and much-restricted free flow. After flowing for some 50 km through the classical oasis of el-Ghutta, the Barada River ends in the Syrian desert in the terminal Lake Utaybah. The Awaj River, in its turn, ends in the terminal Lake Hijaneh.

Farther into the Syrian desert, the mountain range of the Palmyrides (Jabel ar-Ruwaik), a tectonic fault associated with the early stages of rifting, feeds the important karstic spring of 'Ein al-Afqa, the life-giving source of classical Palmyra, today's Tudmur. At present, the spring discharges a mere 2 million cubic meters per year.

In Lebanon the rift valley is divided into the Jordan fault to the south and the Orontes fault to the north. Between them lies the mountain valley of Bekaa (the classical Coelesyria) at an average elevation of 800 m. The Litani River flows south of the 1,100-m-high drainage divide of Baalbeq, in what in fact belongs to the Jordan graben. Its most important headwater spring is the subterranean karstic drainage of the dolina lake Amik Gölü (Lake Amik, Lake Antioch). However, the discharge of the Litani also very much depends on the contribution of surface runoff brooks. The Litani flows south for about 40 km in parallel with the Hasbani River, and then abruptly turns to the west, crosses the Lebanon Mountain range, and empties in the Mediterranean, like other littoral rivers of Lebanon. It even changes its native name to the Qasmieh River. The ridge that separates the Litani from the Hasbani today is only 5 km wide.

The Orontes River or Nahr el-Assi, "the unruly river," starts its northbound flow only a few kilometers from the sources of the Litani, in the strong spring of 'Ein Zarqa, described by Weulersse (1940) as "une rivière qui naît d'elle-même." The output of 'Ein Zarqa is over 200 million cubic meters per year, comparable in volume and stability to the Dan. The Orontes crosses the basaltic barrier of Homs and then emerges in the younger segment of the rift valley, called the el-Ghab. In this swampy depression, additional artesian springs flow in, with a combined output even higher than that of 'Ein Zarqa. The last artesian spring, the classical spring of Daphne, is found near the ruins of Antioch. Here, the Orontes, diverted by the ridge of Jisr el-Hadid, abruptly turns to the west, where it used to receive the outflow of Amik Gölü, before descending steeply to the sea, in some stretches dropping more than 5 m per 10 m of flow. Also being fed by artesian sources along its entire course, the Orontes shows practically no seasonal fluctuation in its water budget.

Amik Gölü itself, drained in stages after the 1930's, was fed by rivers that descend from the Taurus Mountains. Among them, the valley of the Kara Su is considered to represent the northernmost and last extension of the rift valley. Today, all the waters of the lake basin are drained to the Orontes through an artificial channel called "Nahr al-Kowsit."

Zoogeography of the western branch of the Aquatic Crescent

The study of the distribution of the inland water animals in the rivers of the Levant can provide interesting clues for the archaeologists of this region. Looking for instance at the map of the spread of the Pre-pottery Neolithic culture in the Levantine Corridor and the Fertile Crescent as a whole (Bar-Yosef 1998), it is remarkable that it duplicates the distribution maps of the inland water animals in the region (Figure 2). The terrestrial fauna and flora of the Middle East, on the contrary, show different patterns of geographical distribution. It seems, therefore, that human cultures spread through the Middle East, essentially following an "aquatic" pattern of distribution similar to that of the so-called "primary freshwater fauna." To this faunal category belong the fish, the higher crustaceans, and many aquatic molluscs, organisms that need perennial fresh water and contiguous water bodies in order to spread.

There have been frequent changes in the structure of

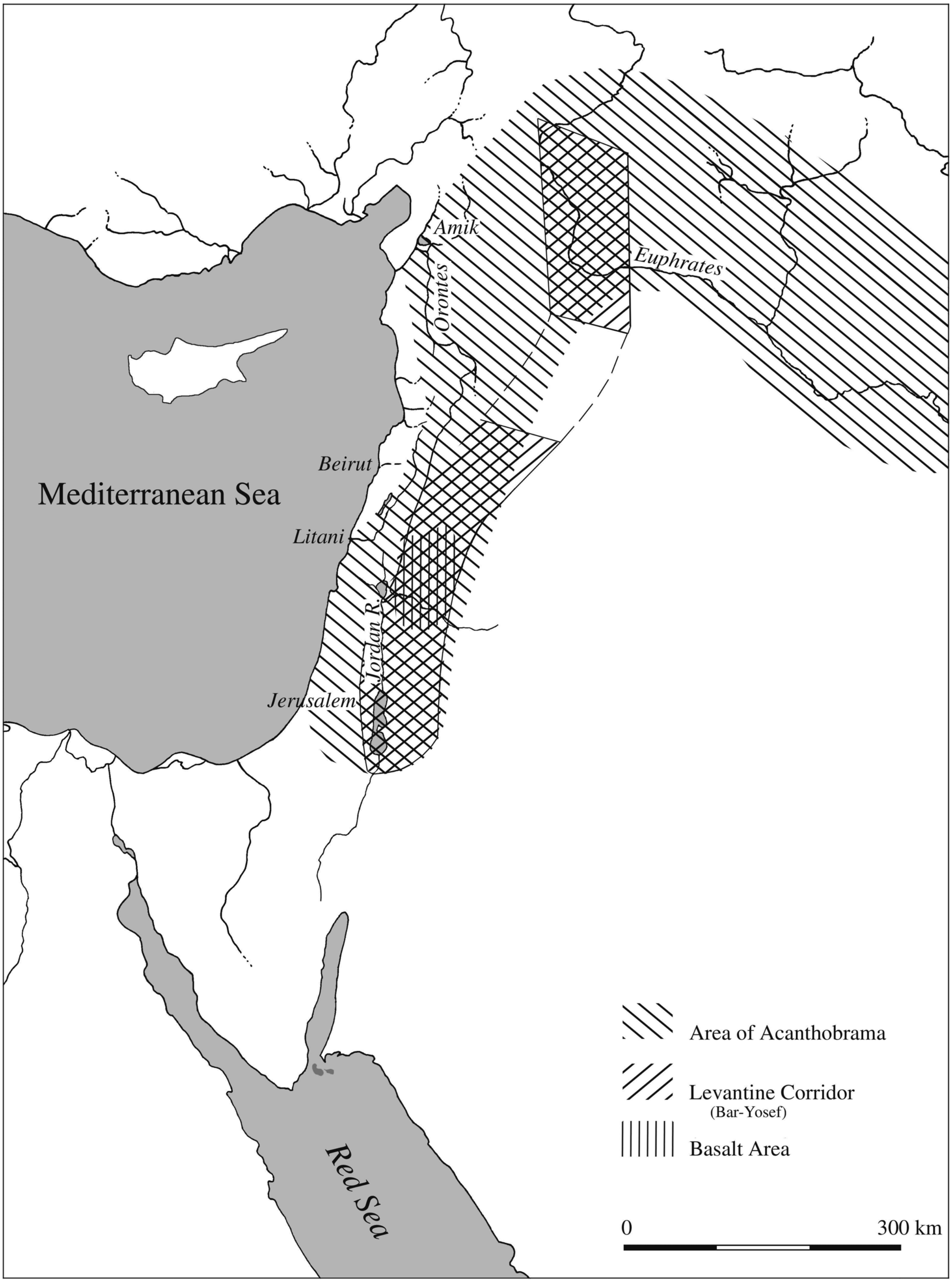
Amik
Orontes
Euphrates
Beirut
Mediterranean Sea
Litani
Jordan R.
Jerusalem
Red Sea
Area of Acanthobrama
Levantine Corridor
(Bar-Yosef)
Basalt Area
0
300 km

Figure 2. Superposition of the distribution of the fish genus *Acanthobrama* and the "Levantine Corridor" *sensu* Bar-Yosef (1998).

the hydrographic net of the Levant, as a result of tectonic movements and accompanying basalt extrusions, of headwater captures, and to a lesser degree of pluviometric climate changes. Many of these past changes are suggested by the distribution pattern of the recent aquatic fauna.

Perhaps the most important tectonic event, besides the extending and deepening of the rift valley itself, was the uplifting of the Palmyride range, which gradually cut off direct contact of the Jordan and Damascus Basins with the Euphrates Basin.

In the Late Pliocene, the nascent Jordan rift valley was occupied by a marine gulf, eventually turning into a salty lagoon, the "Sedom Lagoon" (Horowitz 1979). It probably did not extend north of the present Lake Kinneret. Besides the massive salt extrusions at Mount Sedom, the old Pliocene aquifers of this lagoon still feed a good number of saline springs in the rift valley. Relic biota of this water body, mainly crustaceans, are found today in the subterranean aquatic fauna around the Dead Sea. For example, species of *Tethysbaena* and *Turcolana* have congeners that are found all around the Paleogene Tethys shorelines of the Mediterranean.

The blind prawn, *Typhlocaris galilea*, found in the strong spring of Tabgha 5 on the Kinneret shore, is one of the most important species for preservation among the biota of our inland waters. The congeners of *Typhlocaris* are found in subterranean sites in Cyrenaica (Lybia) and in southern Italy. No marine relics are found in the Hula Basin. The limits of the extension of the Pliocene gulf are thus faithfully documented by the distribution of its relic species.

After the renewed tectonic activity of the Gelasian Pliocene, the marine gulf which occupied the rift valley was replaced by the *endorheic* basin of the Dead Sea, cut off from Mediterranean marine influx. This phase of rifting is impressively associated with a widespread layer of basalt, the so-called "cover basalt," which is dated at around 3 Ma (Mor & Steinitz 1982). As the rifting activity advanced, the shape of the hydrological network changed, with south-north contacts coming to prevail. Freshwater conditions were already established by the time of the Erq el-Ahmar site. The nascent Levantine waterway, supplanting the salt lagoons, was already open to supply trophic support to human migration.

The paleo-endemic sponge genus of the Kinneret, *Cortispongilla barroisi*, is living proof of the fact that fresh water has existed in the rift valley since the Late Pliocene. Other related species of sponges are known from the old Pliocene lakes, Tanganyika, Baikal, and Ochrid. *Cortispongilla* was also present in Lake Hula 20,000 years ago, during its "deep lake" phase (Racek 1974). The small snail *Falsipyrgula barroisi*, which first appeared in the Erq el-Ahmar Formation (Schutt & Ortal 1993), has not been recorded from later sites, but survives today in Lake Kinneret. In general, the first freshwater mollusc faunas of the Jordan Valley are also well documented in the subsequent 'Ubeidiya Formation. Less informative are the much sparser fossil fish finds.

The Levantine waterway turned into a potential two-way distribution pathway for aquatic biota from both the south and the north. However, the Levant waters were colonized primarily by northern or northeastern species. A southern, African influx was present but was much more limited.

Several molluscs, like *Theodoxus jordani*, *Viviparus unicolor*, *Valvata saulcyi*, and a few others, are of African origin (Schutt & Ortal 1993). Also of African origin are the cichlid fishes, the "Saint Peter's fishes." They probably reached the area in very ancient times, since they are found at 'Ubeidiya and since they evolved locally into new genera (*Astatotilapia*) and new species (of the genus *Tristramella*). *T. simonis* even reached the Damascus Basin. More recent waves of immigrant cichlids still continue to reach the rivers of the rift valley. For example, in recent times, *Tilapia nilotica*, swept into the sea by Nile floods, has entered our coastal rivers and, using their headwater contacts, reached the rift valley (Banarescu 1992). The successive waves of cichlid migration thus resemble the successive human migrations out of Africa. Initially and naturally limited to the warm waters of the Levantine rift valley, the tilapias today, with the help of humans, have become worldwide aquaculture species. The African catfish, *Clarias gariepinus*, widespread in the Jordan system, has also reached the Orontes by natural means (Krupp 1987).

African influx is also documented by the Early Pleistocene presence in the Jordan Valley of higher aquatic biota, such as *Trionyx triunguis* (the soft-shelled turtle) and *Hippopotamus* (Tchernov 1988). Like the other African immigrants mentioned above, these were also limited to the Jordan Valley and the coastal rivers of Israel.

Among the species of northern origin, the Levantine endemics stand out. The bleak, *Acanthobrama*, is an endemic fish genus of the rivers of the Fertile Crescent: *A. maramid* inhabits both the Euphrates and the Orontes, while the more isolated Jordan and Damascus Basins have their own endemic species of *Acanthobrama*. The mussel genus, *Leguminaia*, is also endemic to the Aquatic Crescent. In both of these cases the parentage is with northern genera (Banarescu 1992).

The entire northern family of Unionidae mussels, a choice food for our ancestors, reaches its southern limits in the rift valley. Among the most widespread species of this category are the prawn, *Atyaephyra desmarestii*, and the barbel fish, *Capoeta damascina*, extending all the way east to the Jordanian oasis of el-Azraq and to the Mujib River in the south (Kinzelbach 1987). Several of these genera of northern origin do not reach the Jordan Basin at all. However, the Palearctic loaches (Cobitidae), fishes of swift brooks, are widespread, with a number of local species of still unclear taxonomic status. Wadi Qelt near the Dead Sea seems to be the southernmost locality where this family is found.

Tectonic activity and successive local basalt extrusions have continuously changed the shape and contacts of the river basins of the Levant, the general tendency being the deepening of the valley floor and concomitant growing emphasis on the *endorheic* south-north axis.

The fauna of the Litani, the Damascus Basin, and the Jordan Basin are closely connected and, to a significant degree, different from that of the Orontes Basin. This is a strong indication that the first three basins were at times contiguous. The Litani was a tributary of the Jordan until the uplift of the Marj Ayyun block. The Yarmuk, together with the lower Jordan, also had an old outlet to the sea near Haifa along today's Qishon River. At times the Yarmuk was also connected with the el-Azraq oasis in Jordan. The aquatic connection between the Jordan and Damascus Basins was only quite recently interrupted by the basaltic outflow of the Golan Heights. The Damascus Basin, in turn, had a connection to the distant Euphrates, but this contact was probably interrupted already in the Early Pleistocene by the uplifting Palmyride chain. The famous aqueduct built by the Palmyrene queen and empress Zainab (Septimia Zenobia), which brought additional water from the Anti-Lebanon to supply her short-lived metropolis, was perhaps a man-made replay of an old-remembered connection.

The outflow of the Litani to the sea is of fairly recent Pleistocene origin. According to Krupp (1987), the uplift of the Baalbeq ridge separated the old precursor of the Litani from the upper reach of the Orontes, which started to flow to the north.

The Orontes itself was deeply influenced by newer stages of rifting. The present river was established in the Late Pleistocene, when the Ghab Basin progressively deepened, allowing the union of three separate rivers. The downstream segment opened to the sea only in fairly recent times. At times, it was in direct contact with the Euphrates through the basin of the Quwaiq River, the river that fed, and to some extent still feeds, the ancient city of Haleb (Aleppo). The Quwaiq today is an *endorheic* river, ending in a *sabkha*, but it has, or rather had before being polluted, a fairly rich fish fauna. It also used to be inhabited by several species that it shares only with the Euphrates.

The middle segment originally opened to the sea through the present Nahr el-Kalb, before the deepening of the Ghab valley. Finally, the upstream segment of the Orontes, once an independent river, drained into the middle reach after cutting through the basalt barrier of Homs.

The Orontes is home to an astonishing biodiversity of 32 species of fish. Despite this aquatic richness, it is worth noting that very few archaeological sites of Pleistocene age have been found along this river.

Following the path of the aquatic biogeographic pattern, it seems reasonable to assume that human and cultural contact between the two branches of the Fertile Crescent, the rift and the Euphrates, went through the intermediary of the Quwaiq, the old residual river basin of the ancient town of Aleppo.

The desert gap separating Aleppo from the banks of the Euphrates is much narrower than the much older, possibly alternative track which connected the oases of Damascus and Palmyra with the Euphrates. The presently isolated Damascus Basin is still inhabited by 10 species of fish and, symptomatically, by the prawn, *Caridina fossarum*, found only in the distant Euphrates.

Events coeval with Levantine humans

There is little doubt that successive waves of human settlers witnessed the changes undergone by this hydrographic net. Unlike other areas that have been tectonically quiet, throughout the Pleistocene and afterwards the rift valley and surrounding areas have experienced rapid and dramatic changes and even cataclysmic events. Humans witnessed processes of uplift and subsidence and the environmental changes induced by these movements. While permanent water bodies existed throughout the Pleistocene, fed by the karstic exsurgences, the rivers often changed their course, and the extent and depth of the lakes were continually shifting and changing. Although fresh water was always in supply, there nevertheless was a permanent short-term dynamism to which humans had to adapt.

Perhaps the most dramatic changes were the outpourings of basaltic flows caused by the volcanism that accompanied the rifting. The "cover basalt" event in the earliest Pleistocene perhaps marks the renewal of rifting which created the *endorheic* aquatic basins and *ipso facto* opened the migration road to the North.

After this major volcanism, there has been a succession of smaller and more local basalt extrusions. The lacustrine site of Erq el-Ahmar is situated above the cover basalt. Lake Hula in its recent, pre-drainage form probably came into being as a result of the barrier created between 560,000 and 850,000 years ago by the Yarda basalt flow that underlies the site of Gesher Benot Ya'aqov. However, an older lake ("Lake Gadot") is known to have occupied more or less the same location in the Pliocene. The Hasbani basalts, which changed the fate of the Litani, are 70,000–80,000 years old. Much younger dates of ± 10,000 years are given for some of the Homs basalts, and even as late a date as 4,000 years ago is mentioned for the last outpouring of the Golan basalts. It is tempting to see such events as being reflected in the saga of Sodom, Gomorrah, and the other three ill-fated towns. However, there are no indications of volcanism in the area of the southern Dead Sea, where this event has traditionally been placed, whereas there are plenty of extinct volcanoes and extensive basalt traps farther north in the Galilee.

Earthquakes were common occurrences as rift movement progressed and new basins subsided. The site of Erq el-Ahmar is down-warped and the living floors at 'Ubeidiya were tilted almost 90°. The site of Gesher Benot Ya'aqov and the much younger Chalcolithic site of Ghassul also show tectonic tilting. The modern pre-drainage extension of Amik Gölü (Lake Antioch) in today's Turkey, which covered earlier Neolithic and Chalcolithic sites, is possibly related to the severe earthquake of 550 AD.

Lake levels depended on tectonism and basalt barriers, as well as on shifting river supply. A lake in the Lebanese Bekaa was drained when the Litani broke through to the Mediterranean. The Orontes cut through the basalts of Homs when the Ghab Valley subsided tectonically. The large lake in the Ghab drained when the Orontes opened up to the Mediterranean.

Lake Hula, a stable presence since the later Pliocene because of its rich supply of karstic aquifers, also presents an eventful history. In the later part of the Pleistocene, around 20,000 BP, the lake reached a maximum extension and possibly a depth of 10 m. In the north of the Hula Basin, the Dan River turned into a near-shore source for this lake. Around 16,000 BP, this extended Lake Hula drained in part through the basalt barrier of Benot Ya'aqov, most likely when the basin of Lake Kinneret deepened and a new hydrographic base level was established in this *endorheic* basin. At their maximum extension, the Hula swamps probably covered 100 square kilometers or more, quite a sizeable alluvial plain given the topographic conditions of the narrow rift valley.

Little is known of the earlier Pleistocene history of the Dead Sea Basin, but it too must certainly have undergone repeated tectonic subsidence in order to reach its present lake bottom level of nearly -800 m. During the last Interglacial, a shallow lake ("Lake Samra") occupied its basin. In contrast, between 70,000 and 15,000 BP, a large and deep lake, the so-called "Lake Lisan," occupied the area. For a short while this lake extended far beyond the present limits of the Dead Sea to include the Kinneret Basin. For most of its existence, this lake, 150 km long by only about 15 km wide, very much resembled an African rift valley lake. The level of Lake Lisan was much higher than the present Dead Sea level of circa -400 m. It rose in various phases, interrupted by lower levels, and for a brief period between 26,000–23,000 BP reached a maximum of only -164 m, i.e., more than 200 m above the present level. The salinity of the Lisan was much lower than that of the present practically abiotic Dead Sea waters, but it was still saline enough to limit sharply the diversity of its aquatic biota (Begin et al. 1974). Lake Lisan contracted and split into several lakes around 18,000 BP. The Dead Sea reached a minimum level of more than -440 m around 11,000 BP. Afterwards, around 6,700 BP, the level rose again to -280 m. A relatively stable level of around -400 m was attained only after 4,800 BP (Bartov et al. 2001). Between 40 BC and 100 AD, an abrupt rise of nearly 70 m in the level of the lake reached the site of Qumran and, according to Klein (1986), might have induced the members of the Essene sect to protect their parchment scrolls by storing them in caves at higher elevation.

There are various factors that must have contributed to this eventful history of the Dead Sea. Change in river inflow, pluvial conditions, limited evaporation rate during cold spells, and finally tectonic deepening of the basins must all have played a role.

Lake Kinneret, which existed in some form prior to the brief invasion of the Lisan waters, once again became an independent, slightly brackish lake, some 40 m deep, in its own trench nearly 250 m deep. In the Bet Shean area, a third shallow lake existed until around 5,000 BP, when the young down-cutting lower Jordan River drained it.

During the relatively short existence of the expansive saline Lake Lisan, the conditions along its shores must have been fairly inhospitable for significant human settlement. Probably no fish and no molluscs lived in the salty lake and, as a consequence, bird and mammal life must have been restricted as well. There are fossil reports of various species of diatoms in this lake, meaning that some invertebrates must also have lived there (Begin et al. 1974). Lake Lisan must have functioned, therefore, as an important barrier for human migration. Its sibling, Lake Turkana, in the African stretch of the rift valley is another terminal desert lake, but one that is only slightly saline and still supports a fairly diverse aquatic fauna.

There may have been an alternative route for human migration in Transjordan, where several shallow terminal lakes, like the extensive Lake Jafr and another lake in the el-Azraq oasis, existed during the later phase of the Last Glacial. These lakes also shrank around 18,000 BP, but had a short rebound around 8,000 BP. Jafr is presently a seasonally water-covered *sabkha*, and Azraq maintains a small perennial water body.

Like Lake Hula, the terminal lakes of the Damascus Basin also attained their maximum extent around 20,000 BP. It seems that for the very labile systems of these terminal lakes the reduced evaporation rate during the cold Glacial climate, rather than increased precipitation, must have been the decisive factor.

Riparian cultures of the Levant

Bar-Yosef (1989) emphasized that the smooth transition to the sedentary communal life of the Natufian, and afterwards to cultivation and to the Pre-pottery Neolithic, was a specific and autochthonous phenomenon of the Levant. Anfruns & Molist (1997) mentioned the importance of the rivers and alluvial plains as a prerequisite for high population density and cultural continuity in the Levant. Wedged between a poor oligotrophic sea and the unproductive desert, a broad-spectrum economy (Flannery 1971) could develop only along the axis of the rift valley wetlands. There was no "fertile land along the Mediterranean coastline" (Eastman 2002).

Earlier Paleolithic bands of hunter-gatherers could take advantage of the diversity of resources provided by the proximity of four biotic-climatic zones in the Levant, namely the Mediterranean, Saharan, Irano-Turanian, and Sudanian zones. In one day's walk they could cross from the sea, through the Cis-rift mountains, and down to the rift valley. They could also benefit from the drinking water supplied by small mountain springs and brooks.

However, the economic backbone that supported the novel cultural evolution of large sedentary human concentrations in the Late Pleistocene of the Levant is likely to have been provided by the existence of a durable riverine corridor, maintained by the strong artesian springs of the rift valley. The Natufian and pre-pottery Neolithic villages, based on nearby perennial wetlands, could have long and undisturbed histories of hundreds or even thousands of years. In some of them the transition to plant breeding and to Neolithic industry could arise smoothly, as a local development.

It was first and foremost because of the proximity to spring-fed streams, rivers, and lakes that large sedentary communities could develop a "broad spectrum" economy (Flannery 1971), in which fish, molluscs, and amphibians, together with birds and mammals, cereals, and other wild plants growing on the rich alluvial marshland soils, formed the diet of the Natufian hunter-gatherers. In due time the first experiments with plant cultivation were carried out there.

The artesian springs and spring-fed brooks have a stable output that is only in part dependent on runoff . Furthermore, these springs maintain a stable temperature throughout the year, for instance 16°C in the Dan. The spring of 'Ein Mallaha ('Enot 'Eynan) forms a spring pool in which temperatures are stable at 21–22°C the year round. The stream of 'Eynan and its spring pool provided a refuge from winter temperatures of 5–6°C, lethal for the fish populations of Lake Hula and its swamps. It also served as a homeothermic refuge when summer temperatures rose too high and oxygen became scarce in the water. The existence of this spring refuge guaranteed the welfare of the rich fish populations of the lake. The inhabitants of Mallaha must have taken full advantage of the fish schools crowding in the spring pool at their doorsteps. Migrating birds visiting the lake and the swamps also fed on the rich fish stocks.

In the permanent spring-fed rivers of the Levant, the fish, especially barbels, migrate seasonally in search of more suitable, lower temperatures for spawning. The humans could amply exploit these regular movements of the fish stocks.

The wetlands of the Hula were known for centuries as the best hunting grounds in the region. Besides the birds, rich mammal life concentrated in the swamps and around the pools. The same goes for the wide belt of riparian wetlands of Lake Kinneret and the floodplain of the lower Jordan, after the retreat of Lake Lisan.

Interestingly, the people of Ohalo II, a site until recently covered by Lake Kinneret, fed intensively on the products of the lake, although the site dates to about 19,000 BP, probably shortly after the retreat of Lake Lisan from its northernmost extension. Ohalo II is possibly one of the earliest permanent village-like settlements known in our area. The people there fed on wild barley and wheat, on fish, and on birds, in addition to larger mammals like gazelles (Nadel & Werker 1999). During the climatic crisis of the Younger Dryas, when upland hunting grounds underwent large-scale aridification, the importance of the riparian wetlands and their biotic resources became even more crucial.

On the lower Jordan, several sites like Netiv Hagdud (Bar-Yosef & Gopher 1987) and Jericho relied on the river marshlands in their experimentation with cultivating cereals and other plants. Netiv Hagdud probably used the waters of the spring of 'Ein Duyuk and the wetlands of the nearby delta of the Jordan, which emptied into the high-level Dead Sea of those times. The ornamented pebble found at Netiv Hagdud, if interpreted correctly, probably does not represent a snake but is a faithful rendering of the meanders of the Jordan in the marshlands of the Zor, a crude map for fishermen.

Natufian and Neolithic Jericho depended on the artesian spring of ʼEin el-Sultan and on the wetland of the stream of Wadi Qelt. Situated dangerously near the shore of the Dead Sea, it is possible that the earliest earthen walls of this settlement were built, as suggested by Bar-Yosef (1989), as a protection against episodically rising sea levels rather than tides of unfriendly humans.

The Natufian people of Mount Carmel were probably dependent, at least in part, on resources from the marshland of Kebara, fed by several strong springs of the Tanninim aquifer and by the Tanninim River itself.

The Barada River in the Damascus Basin is a smaller replica of the Jordan. When the large terminal lake receded, the Natufian settlement of Tell Asswad was established in the hills overlooking the marshlands of the two terminal lakes, Utaybah and Hijaneh. Another settlement of the Natufian and early Neolithic has been found at Saidnaya in another river valley descending from the Hermon (Moore 1978).

As a whole, the mountainous stretches of the Litani and upper Orontes do not open up to form significant riparian lowlands. The rivers in this portion are deeply incised mountain streams. Only when the classical Egyptians built the first dam at Homs could the waters of the upper Orontes be used for irrigation purposes. It is therefore surprising that the extensive marshlands of the Ghab have not as yet yielded Natufian settlements. This may be due to lack of archaeological research, or perhaps to the fact that the lowlands of the Ghab are of very recent origin. Nevertheless, important classical towns like Ebla and Apamea developed on the Orontes.

In the far north of the rift valley, Amik Gölü (Lake Antioch) was accompanied by a wide halo of wetlands, not unlike Lake Hula.

Cultural contacts with the riparian Natufian settlements of Tell Abu Hureira and Mureybat, overlooking the floodplain of the middle Euphrates, were most likely possible through the valley of the Quwaiq River, in the area of Aleppo, which was once a river very rich in fish. As mentioned above, this river has been the biogeographical bridge that connected the rivers of the rift valley with the Euphrates system, and the western with the eastern branches of the Fertile Crescent.

The limited area of the floodlands in which incipient riparian agriculture could develop along the Levantine waterway must have confined it to a form of kitchen gardening, which could not produce yields sufficient for a predominantly agrarian population. Therefore, the extensive culture of cereals moved to the steppe highlands of the Middle East, overlooking the Tigris and Euphrates, as soon as the postglacial Climatic Optimum permitted it.

It is remarkable how the occupants of the relatively few artesian springs and favorable wetland areas in the Levant held their ground for hundreds of years, without visible signs of destruction and alien conquest. Moreover, there is evidence of remarkable cultural continuity extending from Beidha in the far south of the rift valley to the villages on the Euphrates (Bar-Yosef 1989). There must have been a very strong organization of federated tribes in order to protect not only their villages, but also their precious springs, wetlands, and fields. Again, the oasis of the Barada River near Damascus provides a hint of the ancient conflicts. According to tradition, it was there that Abel, the good nomad herdsman of the Bible, was killed and buried by the ancestor of all farmers, his brother, the vile Cain.

Environmental challenges

Archaeologists and limnologists are often in the same boat when facing the recent manmade changes in the Levantine waterway. Although most of these anthropic changes are damaging, some of them can yield unexpected positive results. Faced with the need to react to these radical man-made changes of modernity, both groups of scientists are engaged in a frustrating race against time.

Barring water pollution and hasty and irresponsible land-moving activities, the modern changes often duplicate past natural situations. In general, the main factor involved in the environmental changes is the need of the local economies for fresh water, which has increased incommensurably. Therefore, the recent anthropic changes, in a sense, duplicate the limnological conditions of the dry Glacial or, perhaps more precisely, that of the arid Younger Dryas.

For instance, the Dead Sea has been shrinking recently at a rate of nearly 1 m per year and the lake level is now -417 m, more than 10 m lower than in recent decades, nearing the historical post-Lisan minimum and the low level recorded in 1929. As a result, the shallow southern basin has turned into a *sabkha*, a terminal salt pan, artificially converted into salt-extraction ponds. The shore has receded in places by more than 1 km.

This is a golden opportunity to try to locate the five cities supposedly destroyed by brimstone and fire, or perhaps to find significant non-biblical archaeological sites. The result, so far, has been negative. For limnologists it is an opportunity to study the endemic subterranean fauna of the springs that had previously been drowned by the higher Dead Sea level (Dimentman & Por 1991).

The present low level of the sea results mainly from the drastic reduction of the Jordan inflow into the Dead Sea. The Yarmouk, one of the major suppliers, is now almost completely retained behind dams and used both in Syria and for the irrigation channel of the Ghor Project in Jordan. Lake Kinneret, too, has been closed by a dam at the outlet to the Jordan and transformed into a reservoir. Efforts are being made to lower the salinity of the Kinneret in order to supply water of improved quality for the Israel National Water Carrier, which pumps water from the lake. Saline springs, such as Tabgha, are diverted directly into the lower Jordan, which is now saltier than it has been since Lake Lisan times. As a result of Lake Kinneret's lowered salinity, new biota have appeared that are more adapted to true freshwater conditions. The increased use by the Water Carrier, together with the decreased runoff of recent drought years, has often led to an almost catastrophic lowering of the lake level. On the positive side, this has led, among other things, to the discovery of the site of Ohalo II. However, the fauna of the littoral boulders of the lake, the endemic *Cortispongilla* included, face possible extinction.

On the upper Jordan, earth moving related to the regulation of the basin of Lake Hula and the Jordan outlet has damaged the site of Gesher Benot Ya'aqov. The lake itself was drained in 1958 and the stream of 'Eynan, which ran continuously for tens of thousand of years, was completely captured. The village of 'Ein Mallaha lies in ruins. With the demise of the Hula, several endemic biota, like the water vole, *Arvicola terrestris hintoni*, found at 'Eynan, the painted frog, *Discoglossus nigriventer*, the bleak, *Acanthobrama hulensis*, and the cichlid, *Tristramella intermedia simonis* (Dimentman et al. 1992), have disappeared. No archaeological sites have been discovered in the bed of the drained lake and swamps, indirectly proving the long historical continuity of the lake.

The Dan River has been partially captured, below a short stretch of free torrential flow that has been bitterly defended by environmentalists. The Hasbani River is a bone of contention between the pumps of Israel and Lebanon and a potential *casus belli* between the two states. The canalized stretch of the upper Jordan was therefore often deprived of clean water in the summer, carrying only domestic and agricultural sewage. In the last decade, a stretch of the Jordan has been resuscitated and allowed to supply clean water to a small area of the old Hula swamps, named Lake Agmon, which has been flooded again. As in the times of our ancestors of 'Ein Mallaha, once again catfishes and cichlids are fished in the resuscitated lake and countless flocks of cranes and ducks visit the little lake, either wintering there or stopping over on their migration.

In Syria, the Barada River, or what remains of it, is severely polluted by sewage. Excessive pumping has reduced the output of the springs (The Syria Report, March 2002). The Ghab swamps are completely drained and the Orontes is retained in an artificial channel, 60 km long, between the dams of Rastan and Muhardeh.

Between 1958 and 1967, the valley of the Ghab was turned into a 46,000-ha chessboard of irrigated lots, without any recorded effort to locate archaeological sites. Reservoir lakes, like Lake Rastan, were built in the valley. The recently ill-fated Zeyzoun hydroelectric plant also uses water from the northern Orontes. Several species of fish and molluscs, endemic to the Orontes, are in danger of disappearing. Much of the Quwaiq has been retained behind a dam at its headwaters in Turkey and in the 1970's the river ceased to reach Aleppo altogether.

On the sunnier side, the emergent bottoms of Amik Gölü, whose draining in the 1930's led to the disappearance of many species of animals, some of them unnamed victims of extinction, is now subject to intensive research. It has already yielded several interesting archaeological sites, excavated by the Oriental Institute of the University of Chicago. Obviously, the lake is very recent in origin, covering archaeological sites that are now accessible.

Finally and happily, the important sites of Abu Hureira and Mureybat on the Euphrates were investigated in the nick of time before being submerged by the huge reservoir of Lake Assad.

For both limnologists and archaeologists, there is a need to preserve the springs and wetlands as actualistic models in order to be able to understand and restore the environments of the past. Both archaeologists and limnologists are also aware of how dangerous it is to tinker with the environment. We have the hindsight that gives us the tools with which to evaluate the dimensions and consequences of such changes.

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References

Anfruns, J. & Molist Montañà, M. (1997). Prácticas Funerarias en el Neolítico de Siria: Análisis de los Documentos de Tell Halula (Valle de Eufrates). In (J.-L. Cunchillos, J. M. Galán, J.-A. Zamora & S. Villanueva, Eds.) *El Mediterráneo en la Antigüedad: Oriente y Occidente, Actas del I Congreso Español de Antiguo Oriente Próximo*. Madrid: Centro de Estudios del Próximo Oriente.

Banarescu, P. (1992). *Zoogeography of Fresh Waters, Vol. 2. Distribution and Dispersal of Freshwater Animals in North America and Eurasia*. Wiesbaden: Aula Verlag.

Bar-Yosef, O. (1998). The Natufian Culture in the Levant, threshold to the origins of agriculture. *Evolutionary Anthropology* **6**, 159–176.

Bar-Yosef , O. & Gopher, A. (1997). An early Neolithic village in the Jordan Valley, I: The archaeology of Netiv Hagdud. *American School of Prehistoric Research Bulletin* **43**, 247–266.

Bar-Yosef, O. & Tchernov, E. (1972). *The Palaeo-Ecological History of the Site of 'Ubeidiye*. Jerusalem: Israel Academy of Sciences and Humanities.

Bartov, Y., Engel, Y. & Stein, M. (2001). Lake-level and sequence stratigraphy of the Late Pleistocene Lake Lisan, Dead Sea Basin. *Geological Society of America Annual Meeting* (Abstract).

Begin, Z. B., Ehrlich, A. & Nathan, Y. (1974). Lake Lisan, the Pleistocene precursor of the Dead Sea. *Geological Survey of Israel Bulletin* **63**, 1–60.

Dimentman, Ch., Bromley, H. J. & Por, F. D. (1992). *Lake Hula: Reconstruction of the Fauna and Hydrobiology of a Lost Lake*. Jerusalem: Israel Academy of Sciences and Humanities.

Dimentman, Ch. & Por, F. D. (1991). The origin of the subterranean fauna of the Jordan-Dead Sea Rift Valley. *Stygologia* **6**, 155–164.

Eastman, J. (2002). Origins of agriculture in SW Asia. Department of Anthropology, East Carolina University, Greenville, NC (*http://core.ecu.edu/anth/eastmanj/levant.htm*).

Flannery, K. (1971). Origins and ecological effects of early domestication in Iran and the Near East. In (S. Struever, Ed.) *Prehistoric Agriculture.* New York: Natural History Press, pp. 50–79.

Geyh, M. A. (1994). Paleohydrology of the Eastern Mediterranean. In (O. Bar-Yosef & R. S. Kra, Eds.) *Late Quaternary Chronology and Paleoclimates of the Eastern Mediterranean*. Tucson, AZ and Cambridge, MA: University of Arizona, Department of Geosciences, Radiocarbon and Harvard University, Peabody Museum, American School of Prehistoric Research, pp. 131–145.

Goren-Inbar, N. (1998). Gesher Benot Ya'aqov: The Acheulian cultural sequence. *Journal of Human Evolution* **34**, 3–8.

Kinzelbach, R. (1987). Faunal history of some freshwater invertebrates of the Northern Levant (Mollusca, Crustacea). In (F. Krupp, W. Schneider & R. Kinzelbach, Eds.) *Proceedings of the Symposium on Fauna and Zoogeography of the Middle East*. Mainz: Beihefte zum TAVO A **28**, pp. 41–61.

Klein, C., 1986. *Fluctuations of the Dead Sea and Climatic Fluctuations in Erez-Israel during Historical Times*. Unpublished PhD Thesis, Hebrew University, Jerusalem.

Krupp, F. (1987). Freshwater ichthyogeography of the Levant. In (F. Krupp, W. Schneider & R. Kinzelbach, Eds.) *Proceedings on the Fauna and Zoogeography of the Middle East*. Mainz: Beihefte zum TAVO A **28**, pp. 229–237.

Moore, A. M. T. (1978). *The Neolithic of the Levant.* Unpublished PhD Thesis, Electronic Compendium, Oxford.

Mor, D. & Steinitz, G. (1982). K-Ar age of the Cover Basalt surrounding the Sea of Galilee. *Geological Survey of Israel* Frep.ME/6/82, 1–14.

Nadel, D. & Werker, E. (1999). The oldest ever brush hut plant remains from Ohalo II, Jordan Valley, Israel (19,000 BP). *Antiquity* **73**, 755–764.

Perrot, J. (1966). Le gisement Natoufien de Mallaha. *L'Anthropologie* **70**, 437–483.

Por, F. D. (1975). An outline of the zoogeography of the Levant. *Zoologica Scripta* **4**, 5–20.

Por, F. D. & Dimentman, Ch. (1989). *The Legacy of Tethys: An Aquatic Biogeography of the Levant*. Monographiae Biologicae **63**. Dordrecht: Kluwer Academic Publishers.

Racek, A. A. (1974). The waters of Merom: A study of Lake Huleh IV. Spicular remains of freshwater sponges (Porifera). *Archiv für Hydrobiologie* **74**, 137–158.

Schutt, H. & Ortal, R. (1993). A preliminary correlation between the Plio-Pleistocene malacofaunas of the Jordan Valley (Israel) and the Orontes Valley (Syria*). Zoology in the Middle East* **8**, 69–111.

Stekelis, M. (1960). The Paleolithic deposits of Jisr Banat Yaqub. *Bulletin of the Research Council of Israel* **G9**, 61–86.

Tchernov, E. (1975). *The Early Pleistocene Molluscs of Erq el Ahmar*. Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (1988). The biogeographical history of the Southern Levant. In (Y. Yom-Tov & Tchernov, E., Eds.) *The Zoogeography of Israel: Distribution and Abundance at a Zoogeographical Crossroads*. Dordrecht: Dr. W. Junk Publishers, pp. 159–250.

Werker, E. & Goren-Inbar, N. (2001). Reconstruction of the woody vegetation at the Acheulian site of Gesher Benot Ya'aqov, Dead Sea Rift, Israel. In (B. Purdy, Ed.) *Enduring Records: The Environmental and Cultural Heritage of Wetlands*. Oxford: Oxbow Books, pp. 206–213.

Weulersse, J. (1940). *L'Oronte: Etude de Fleuve*. Damascus: Institut Français.

Chapter II
Quaternary Lake Margins of the Levant Rift Valley

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Abstract

The Levant Rift hosted a series of Quaternary lakes and swamps, precursors to or early phases of the Late Holocene Dead Sea, Kinneret and Hula lakes. The margins of these water bodies have been important settings for human activities throughout this period of time. Sediments and fossils that accumulated in and around these lakes record not only the character and dynamics of rift valley communities, but also their environmental context. Three localities in the Levant Rift illustrate the potential of lake margin sites for reconstructing character and change of rift valley environments. The Early Pleistocene site of Erq el-Ahmar preserves vertebrate fossils (and possibly scattered artifacts) in lake margin paleosols. At the Early Pleistocene site of ʻUbeidiya, multiple human occupations are recorded in a series of gravels and pedogenically modified mudstones from the fluctuating lake margin. The Early/Middle Pleistocene site of Gesher Benot Yaʻaqov similarly records multiple occupations of a fluctuating lake margin, with the primary archaeological accumulations associated with beach coquinas. Later Pleistocene and Holocene activities at these lake margins, along with more recent occupation patterns, provide extensive evidence of human adaptations to the lake margin setting. Direct evidence from these sites, coupled with lake histories and regional climatic records, can provide a detailed view of environmental fluctuations throughout the Quaternary of the Levant, and of its effects on human history there.

Why lake margins?

The sedimentary accumulations that occur along lake margins provide a unique archive of terrestrial activities and the environmental settings which shaped them (e.g., Feibel 2001). The sequences produced by sedimentary processes at lake margins both provide direct evidence of hominin lifeways and act as sensitive environmental archives to document the context of these activities.

In the study of the Pleistocene hominin record, lake margins provide much of the direct evidence for behavior and its context. The margins of Quaternary lakes in the Levant were the setting for repeated occupations, accumulating rich assemblages of artifacts. The sites of ʻUbeidiya and Gesher Benot Yaʻaqov (GBY) are among the richest Early Pleistocene localities outside Africa. The habitat characteristics associated with the lake margin ecotone have a rich resource potential, supporting a diverse community of terrestrial and aquatic plants and animals. This clearly was attractive to early hominins, a fact attested to by the repeated occupations at both these localities (more than 80 occupation levels at ʻUbeidiya, more than 21 at GBY). Within the Levant Rift, lake margins form a portion of the hydrologic corridor (Por, this volume) which connected Africa with Eurasia. As such they were an important focus for the movement of both hominins and their technology in the waves of expansion out of Africa.

In addition to their importance as a focus of hominin activity and movement through the Quaternary, the lake margins of the Levant acted as sensitive environmental archives. Lake margins have good burial and preservation potential, within the accumulating basins of the Levant Rift. As transitional zones between terrestrial and aquatic systems, lake margins accumulate a wide range of environmental proxies. The diversity of these signals enable the compilation of multi-proxy records, with the potential of unusual detail in reconstructing both environmental character and change.

Implications

As a result of the diverse data available from lake margin accumulations, it is possible to address two central questions relating to environmental context and hominin evolution: (1) What was the character of the environmental setting for a given occupation or accumulation? and (2) What was the pattern of timing and magnitude of environmental change recorded at the site? In considering these two questions, we can begin to assess local conditions at the sites themselves, the relative significance of regional climate dynamics to human occupations, and aspects of the biogeographic potential of the Rift Valley corridor.

Types of evidence

The evidence of lake margin archives can be considered in terms of four major sources of data: stratigraphy, sedimentology, paleontology, and geochemistry. The stratigraphic data are derived primarily from analysis of individual depositional units, the contacts between units, and evidence of post-depositional modification (particularly soil formation or pedogenesis). This category of data may also include components with time significance, such as magnetostratigraphic records or isotopic age determinations. These may introduce critical chronostratigraphic elements and the potential for temporally based correlation. Analysis of stratigraphic cyclicity may also have significance for related problems of temporal control and correlation. Sedimentological data range from particle size profiles and clast composition to sediment sorting and organization, in association with primary and secondary sedimentary structures. The complexities of the lake margin setting often intermingle a diverse array of sedimentary components, from detrital clasts to biogenic particles and even geochemical precipitates. These may be generated in sub-aerial or sub-aqueous settings, and transported, sorted, and modified through the complex dynamics of the fluctuating lake margin setting. Paleontological evidence spans much of the range of organisms living in or near lake margin settings, probably the most diverse biotic array recorded in a single depositional environment. Individual presence-absence data, numerical abundances, and ecological tolerances all contribute useful data to environmental reconstructions. Geochemistry of organic and inorganic components may add significant quantitative control on environmental parameters, and is especially useful in the analysis of stability or fluctuation in environmental parameters through time.

This analysis focuses on the primary stratigraphic and sedimentological data from 'Ubeidiya and GBY (Figure 1). These data sets allow for an interesting cyclostratigraphic analysis which can serve as a first-order environmental model for testing and refinements based on other proxies. With the additional discussion of reconnaissance work at Erq el-Ahmar, the stratigraphic and sedimentological records demonstrate both the potential and the limitations of serial environmental records with variable temporal calibration.

As a graphic tool for illustrating the environmental fluctuations recorded in these lake margin sequences, a simple model of relative lacustrine vs. sub-aerial influence is employed (Figure 2). In this model, increasing influence of sub-aerial conditions, typically fluvio-deltaic systems or regression, is indicated by arrows impinging from the right side of the diagram. Increasing lacustrine influence, usually an increase in lake level, is depicted by arrows originating along the left-hand margin of the diagram. A rough indication of the relative magnitude of these fluctuations is given by the thickness and length of the arrow. One other feature, for intervals displaying significant pedogenesis (soil formation), is indicated by diagonally cross-hatched lines.

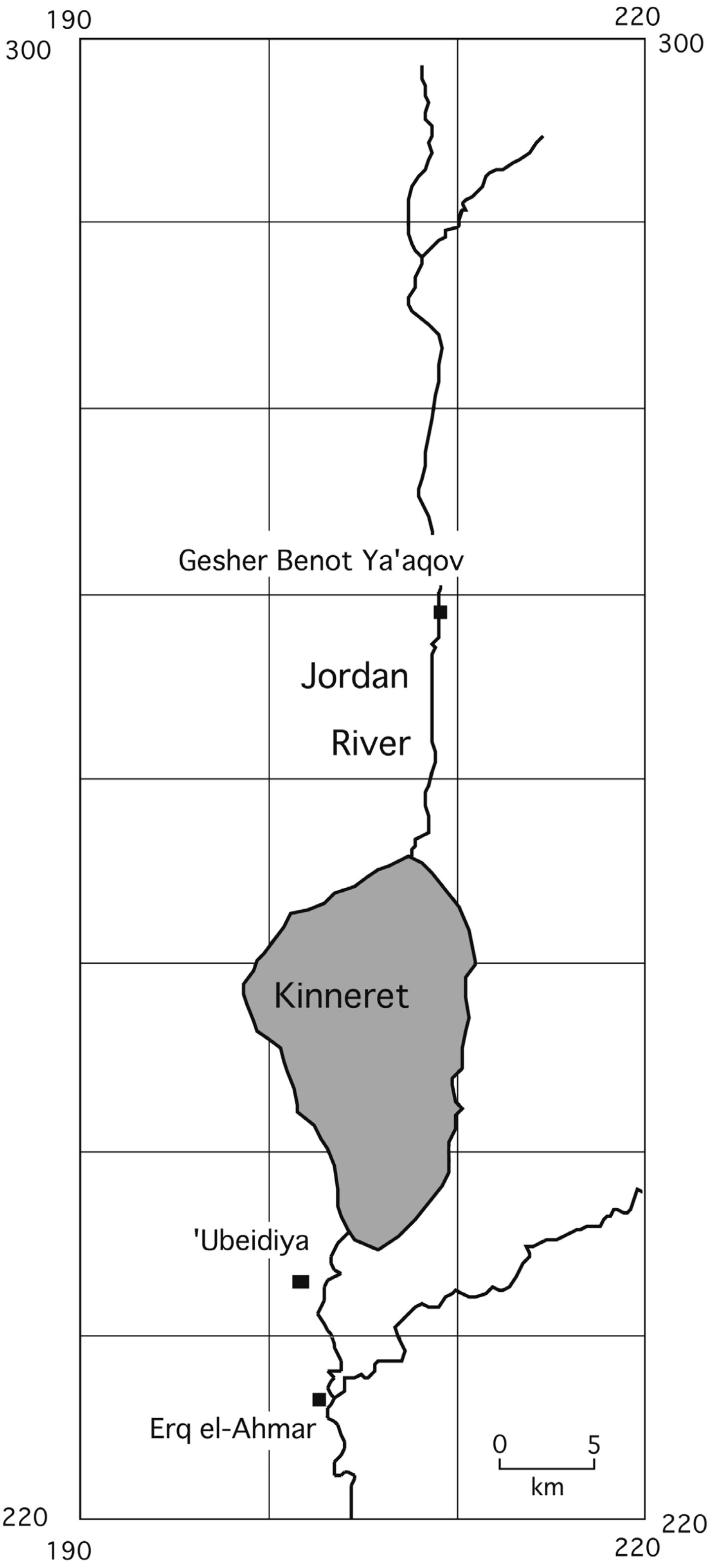
190
220
300
300
Gesher Benot Ya'aqov
Jordan
River
Kinneret
'Ubeidiya
Erq el-Ahmar
0
5
km
220
220
190
220

Figure 1. Location map showing the major sites discussed in the text.

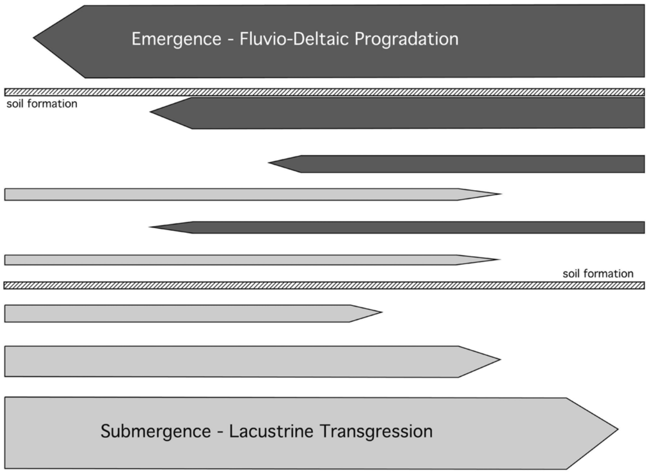
Emergence - Fluvio-Deltaic Progradation
soil formation
soil formation
Submergence - Lacustrine Transgression

Figure 2. Graphic conventions used here to indicate shifting influence of lacustrine and sub-aerial conditions in the interpretation of cyclostratigraphic patterns. Arrows originating along the right-hand margin of the figure indicate increasing sub-aerial control on environmental conditions. Arrows from the left-hand margin indicate increasing lacustrine influence. Thickness and length of the arrows implies a rough guide to relative intensity and/or duration. Lines with diagonal cross-hatching indicate levels where pedogenic modification marks prolonged sub-aerial exposure.

The elephant site at Erq el-Ahmar

The locality of Erq el-Ahmar, long known for its rich molluscan faunas (Tchernov 1975), has been the subject of considerable recent interest as potentially the earliest record of human presence in the Levant (Tchernov 1999; Ron & Levi 2001; Braun et al. 1991). Though much of the Erq el-Ahmar Formation is fully lacustrine in character, some sites expose sediments with well-developed paleosols and terrestrial faunas, such as the partial elephant skeleton excavated by Eitan Tchernov. Lithic artifacts have been recovered from surface prospecting on the formation, and if found *in situ* would document an Early Pleistocene arrival of hominins in the Levant.

The elephant site provides an excellent example of both possibilities and limitations in the interpretation of environmental context of lake-margin localities. At the elephant site, a sequence of some 20 m of sediments is exposed (Figure 3). At the base and top of the section, clear indications of fully lacustrine character are given by fissile

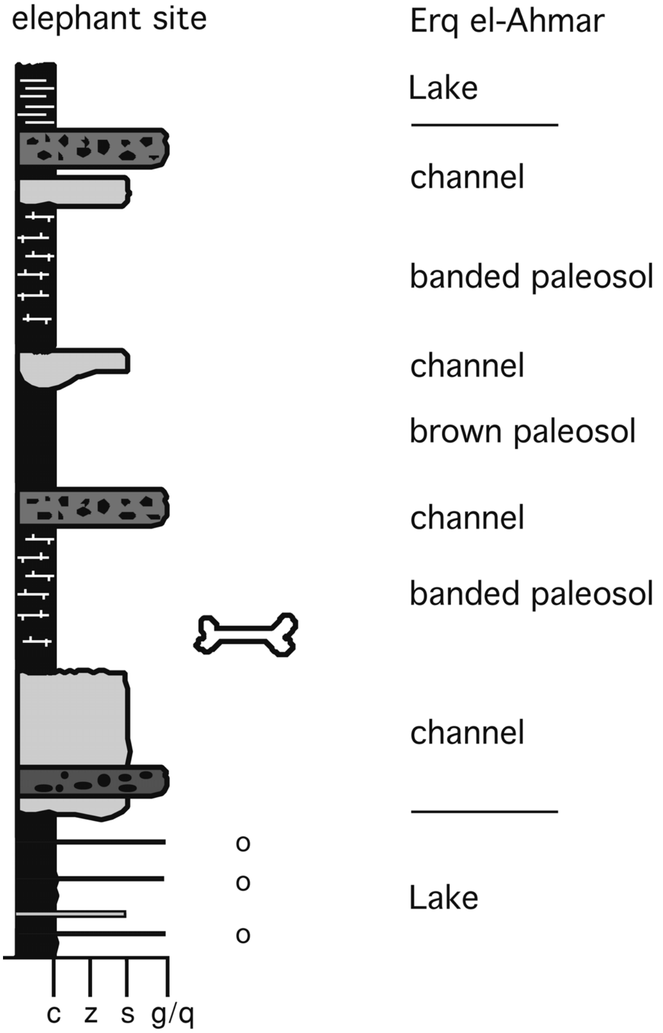

Figure 3. Sketch stratigraphic section from the elephant site in the Erq el-Ahmar Formation, based on description and sampling undertaken in August, 1999.

clays with abundant ostracods and laminites (varves). Between these strata, an interval of interbedded mudstones, sands, and conglomerates demonstrates sub-aerial exposure. At least three well-developed paleosols are recognizable within these mudstones, and the character of the coarser-grained deposits indicates deposition by flowing water. The elephant skeleton was found within the mudstones of the lower paleosol.

The stratigraphic sequence and character of sediments, along with biotic markers (ostracods, molluscs, and fish) and pedogenic features, reflect a shift from fully lacustrine conditions at the base, through exposure and development of a fluvial system (channel and floodplain deposits), and back to fully lacustrine conditions. This can be interpreted as a single first-order cycle in lake-margin dynamics, a transgressive-regressive-transgressive oscillation (Figure 4). Within the lacustrine phases, there are minor shifts in sediment make-up, biotics, and stratigraphic breaks that reflect small-scale variability in the nature of the lacustrine environment. Much of this may indicate the local heterogeneity of the lacustrine setting and short-term ecological dynamics within the lake. Similarly, the fluvial interval demonstrates spatial-temporal dynamics on a floodplain. The channel components often display basal incision and vary in fill makeup (sands and gravels) through the sequence. The paleosols also demonstrate a certain level of variability in character, which may reflect a variety of soil-forming factors (climate, biota, floodplain position, parent material and/or time). There are no clear indications of lacustrine influence through this middle interval, however.

For the specific case of the elephant skeleton, the geological context allows for characterization of the environmental setting. The skeleton was preserved on a floodplain where pedogenesis was active, with small fluvial channels nearby. This setting can be placed in the relative context of a regressive phase of the Erq el-Ahmar lake.

Although the Erq el-Ahmar Formation has been interpreted as lying largely within the Olduvai Subchron (Ron & Levi 2001), there is at present no correlation of the elephant site to the magnetostratigraphic record (based largely on the lacustrine sections). As a result, there is no direct evidence for the temporal placement of the site, or constraints upon the duration of time represented by the exposed sequence. In addition, the brevity of the exposed record, representing a single cycle, gives only a hint of the character of environmental dynamics at the time of accumulation. The thick associated exposures of fully lacustrine strata of the Erq el-Ahmar Formation promise a more complete and longer record of variation through the life of the Erq el-Ahmar lake. The scattered record of terrestrial faunas, along with the tantalizing indications of

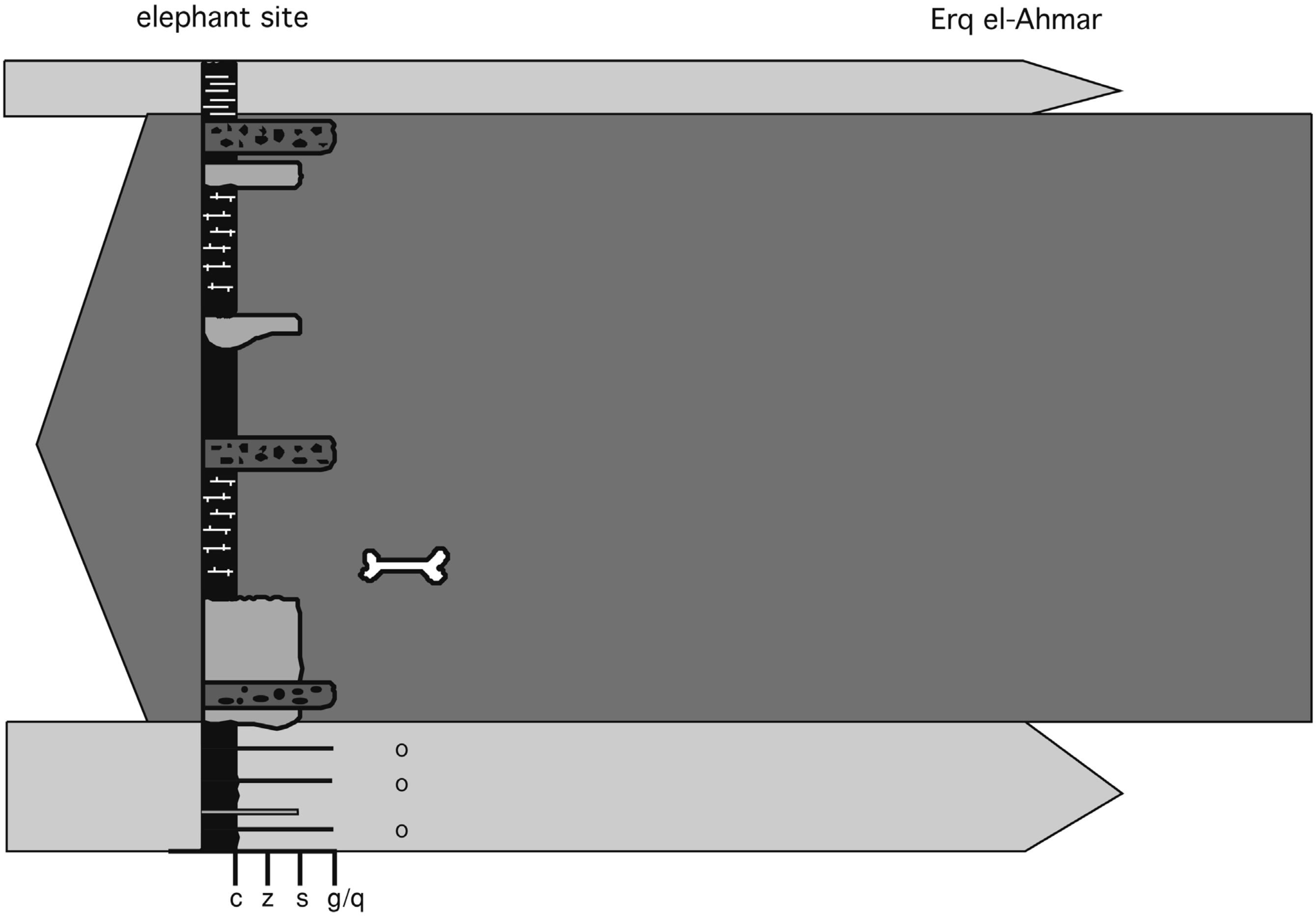

Figure 4. Cyclostratigraphic interpretation of the sequence at the Erq el-Ahmar elephant site. A single first-order cycle from lacustrine to fluvial and back to lacustrine conditions is present. Small-scale variability reflects spatial heterogeneity of the major environments and short-term temporal fluctuations.

lithic artifacts, demonstrate that regressive phases of the lake did indeed archive aspects of terrestrial communities and perhaps early hominin activities, and that there is promise of further and more complete records from the Erq el-Ahmar exposures.

The complex cycles of ʻUbeidiya

The Early Pleistocene site of ʻUbeidiya (Stekelis et al. 1960) is perhaps the best-known early occupation of the Levant (Bar-Yosef & Goren-Inbar 1993). The site has been dated to approximately 1.4 Ma (Tchernov 1987), and comprises a sequence of up to 160 m of lake and lake-margin deposits. Within this sequence, more than 80 occupation levels have been documented (Bar-Yosef & Goren-Inbar 1993). The rich faunal remains, combined with the archaeological wealth and the critical location of ʻUbeidiya in the Levantine Corridor, make it of particular significance to investigations of early hominin movements out of Africa.

Geological investigations of the area around ʻUbeidiya were initiated by Picard in the 1930s, and more detailed work on the sequence began with discovery of the archaeological site in 1959 (Stekelis et al. 1960). The stratigraphic context of the first archaeological excavations at the site was documented by Schulman (Stekelis et al. 1960). Subsequent detailed profiles and sedimentological

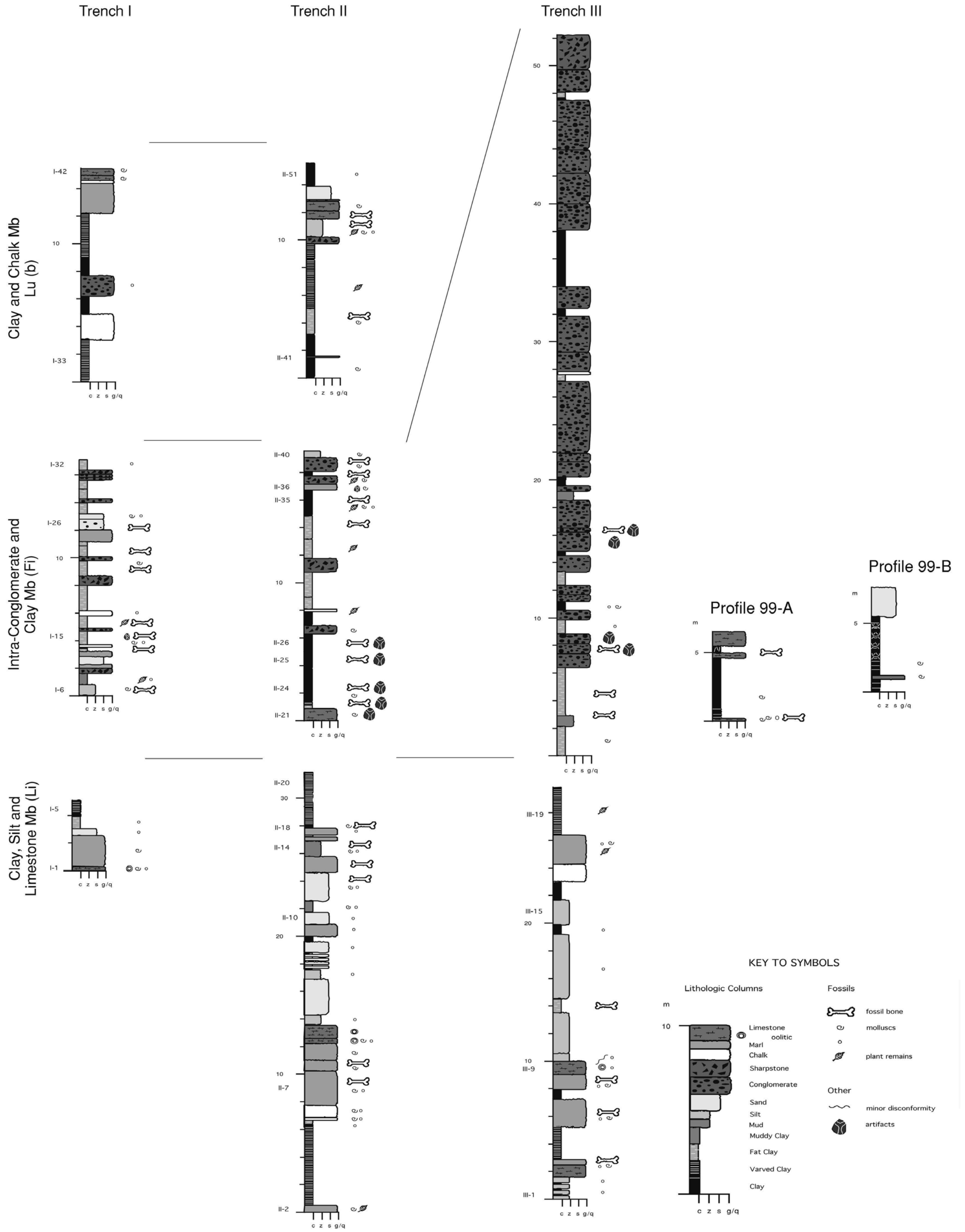
Trench I
Trench II
Trench III
Clay and Chalk Mb Lu (b)
Intra-Conglomerate and Clay Mb (Fi)
Clay, Silt and Limestone Mb (Li)
Profile 99-A
Profile 99-B
c z s g/q
KEY TO SYMBOLS
Lithologic Columns
Limestone
oolitic
Marl
Chalk
Sharpstone
Conglomerate
Sand
Silt
Mud
Muddy Clay
Fat Clay
Varved Clay
Clay
Fossils
fossil bone
molluscs
plant remains
Other
minor disconformity
artifacts

Figure 5. Stratigraphic sections of the ʻUbeidiya Formation, redrawn from Picard & Baida (1966) with additional short sections described and sampled in 1999. Note that Picard & Baida (1966) record only the presence of "bones" in various units, and it is impossible to distinguish between fish and mammalian material from their report.

descriptions were reported by Baida (Picard & Baida 1966). The detailed stratigraphic descriptions from these reports form the primary basis for the discussions to follow. The detailed stratigraphic sections of Picard & Baida (1966) have been redrawn and are presented in Figure 5, along with two short sections described in 1999.

There are two prominent features of the ʻUbeidiya sequence which help characterize both spatial and temporal dynamics of this Early Pleistocene lake-margin setting. The first of these is the high lithologic diversity within the sequence. Picard & Baida (1966) recorded no fewer than 12 distinct sediment types (lithofacies), and many gradations between them (see key to symbols in Figure 5). These range from clays to conglomerates and sharpstones among the detrital clastics, and a wide range of limestones, chalks, and molluscan marls among the carbonates. This is a high level of lithologic variability, and it ultimately reflects the spatial and temporal variability in environmental character through the ʻUbeidiya record. The second prominent aspect of the ʻUbeidiya sequence is the complex cyclicity recorded in repetitive patterns of lithologies. This cyclical nature of the sequence at ʻUbeidiya was recognized early on and formed the basis for the primary division of the formation into members by Picard & Baida (1966). These authors subdivided the sequence into two predominantly lacustrine intervals (Li, Lu) and two predominantly fluvial intervals (Fi, Fu). They also noted that there was a smaller-scale (second-order) variability apparent in the lithologic shifts within members.

The first-order pattern apparent in the ʻUbeidiya sequence clearly reflects two major cycles in the history of the ʻUbeidiya lake (Figure 6). The lacustrine or transgressive component of each cycle is marked by a variety of carbonate facies (marls, chalks, and limestones) and in particular by the presence of varved clays. The fluvial or regressive portion of each cycle is typically dominated by conglomerates and fat clays. At one extreme, the varved clays reflect quiet-water deposition in a relatively deep lake setting (below wave base), while at the other, structural characteristics within the fat clays demonstrate sub-aerial exposure and soil development.

The smaller-scale, or second-order, variability that is apparent within the dominant facies of each cycle reveals a shorter-term pattern of environmental oscillations. Thus, within the lacustrine stages there is ample evidence for exposure and soil formation, while the fluvial stages are punctuated by distinct lacustrine incursions. An example of the pattern seen in these second-order oscillations is shown in Figure 7, using the Trench I record of the Fi Member. Several features of this pattern are of interest. At this level, the oscillations do not appear to be obviously cyclical or periodic. There is a preponderance of lacustrine influence in the lower part of the member, and a shift to more strongly fluvial influence (conglomerates and sharpstones) towards the top. The mudstones are predominantly fat clays throughout the member. Many of these preserve structural features that are clearly pedogenic in origin (e.g., slickensides), but this does not preclude initial deposition by brief transgressive events.

At the next level of analysis, looking at the shifts between individual depositional units, we can examine the immediate context of bone accumulations and archaeological levels. Two examples from within the lower part of the Fi Member serve to illustrate this pattern. Profile 99-A, described in Trench IIb (Figure 8), documents the context of the archaeological accumulations in levels II-21 through II-26. At the base and top of the interval are limestones that reflect short-term lacustrine transgressions. The intervening mudstones are heavily overprinted by pedogenic modification. At least five levels can be recognized on the basis of pebble and cobble lines within the clays, reflecting land surfaces that are locally marked by significant archaeological accumulations. At the immediate site where 99-A was described, the upper and lower surfaces preserve abundant mammalian bone, but both bone and archaeological materials were laterally recovered (see Figure 5).

Profile 99-B, from Trench III (Figure 9), documents the context of the faunal and archaeological materials in unit III-22. Here the waning lacustrine influence can clearly be seen, with the faunal accumulation again within a pedogenically modified mudstone.

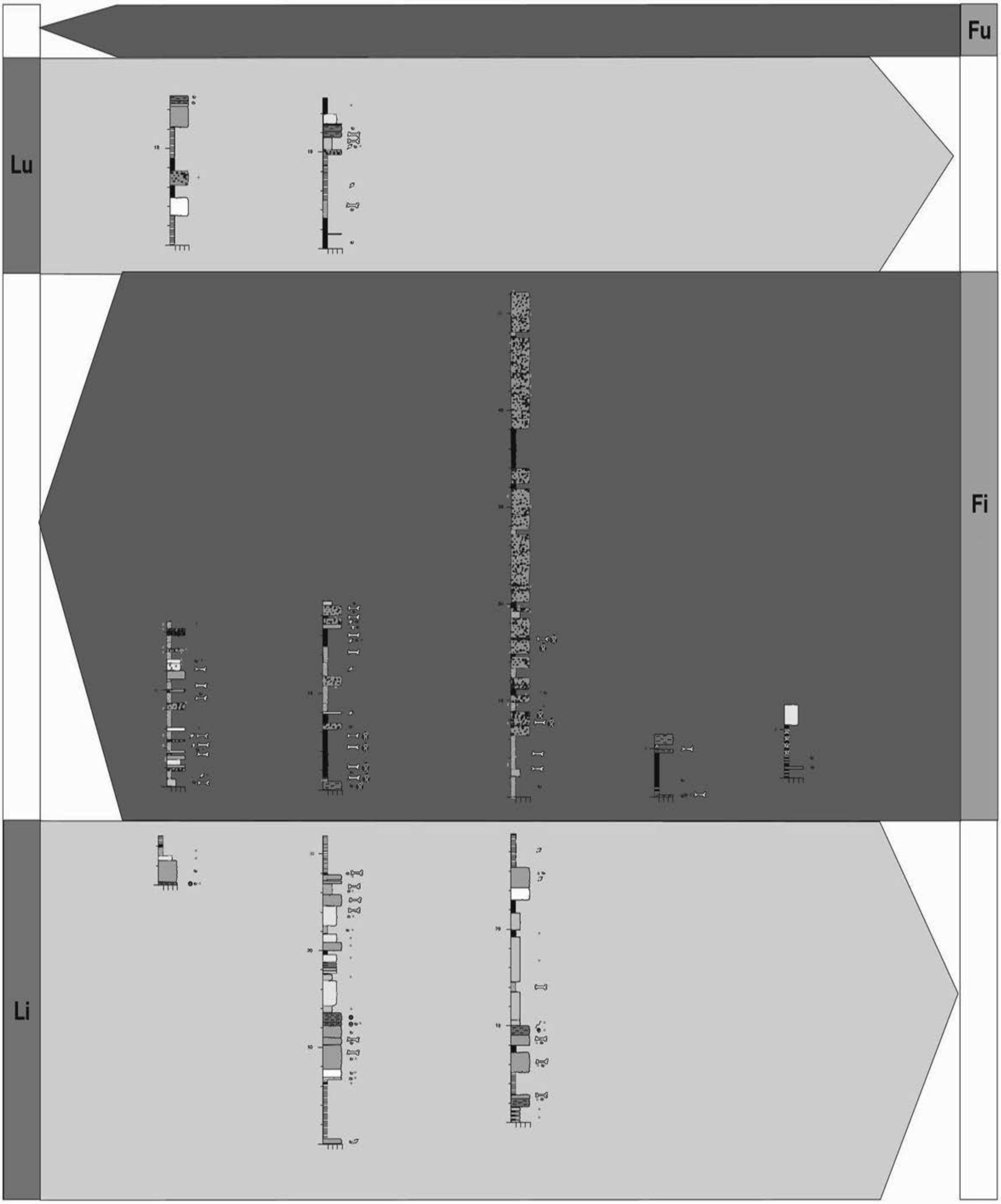

Figure 6. Cyclostratigraphic interpretation of the first-order variability seen in the ‘Ubeidiya Formation.

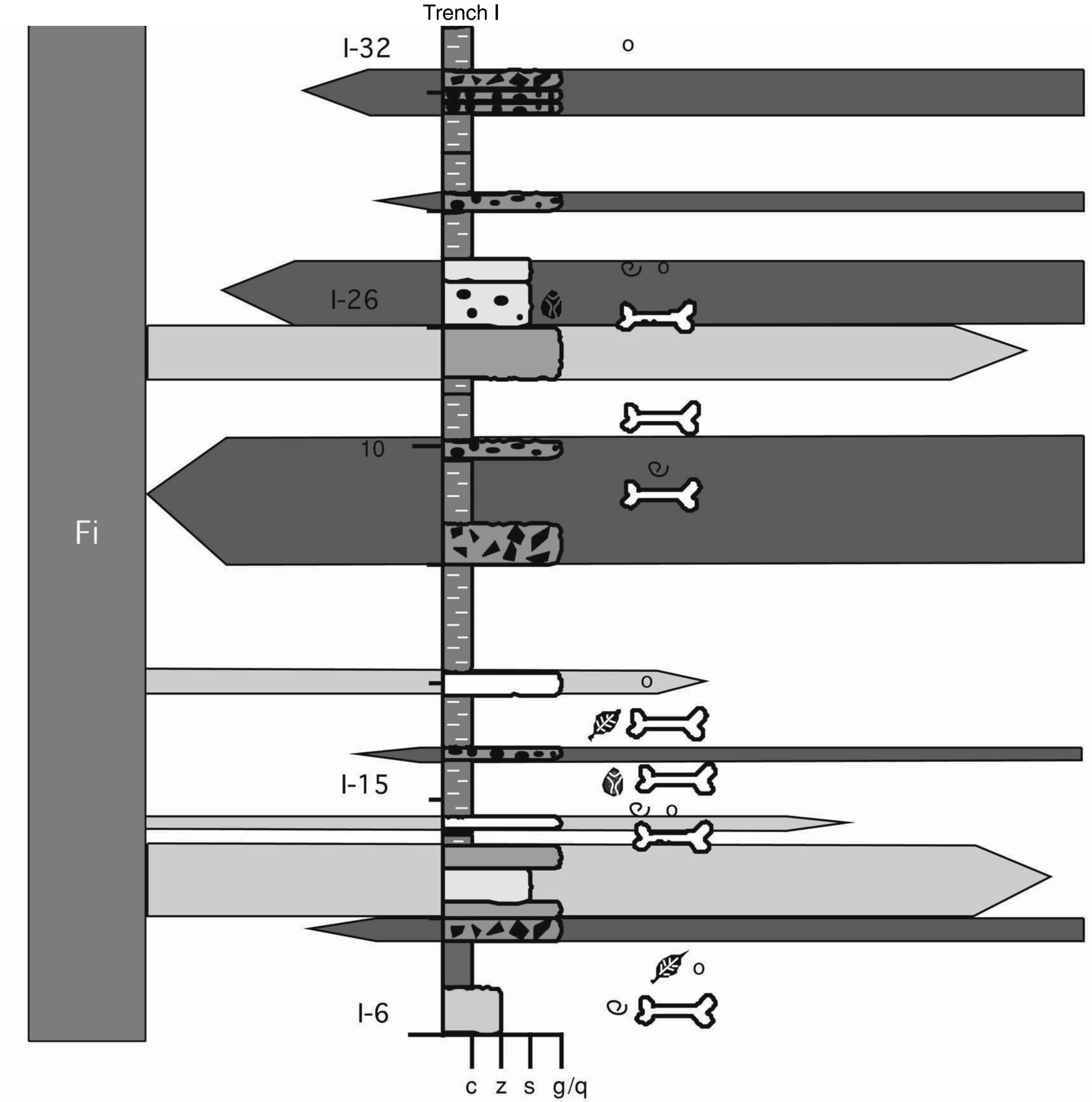
Trench I
I-32
o
I-26
o
10
Fi
o
I-15
o
I-6
o
c z s g/q

Figure 7. ʻUbeidiya Fi Cycle, showing interpreted environmental fluctuations based upon the Trench II record of Picard & Baida (1966).

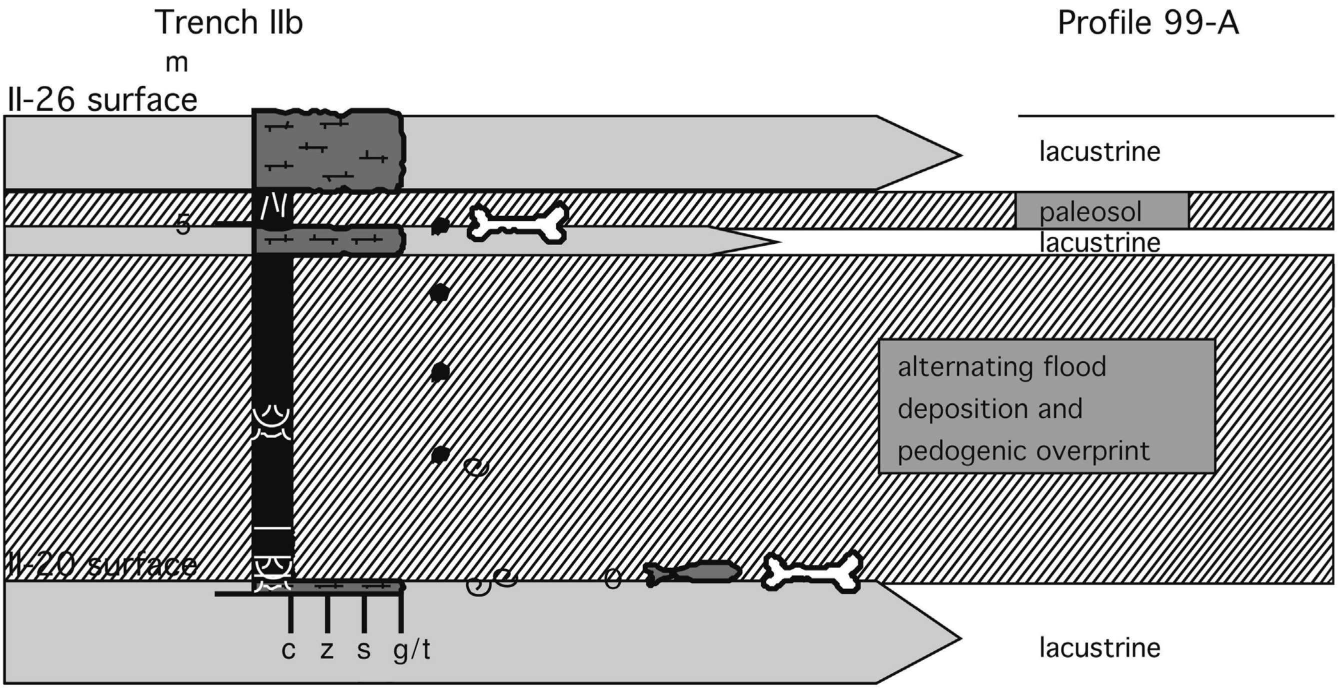
Trench IIb
Profile 99-A
m
II-26 surface
lacustrine
5
paleosol
lacustrine
alternating flood
deposition and
pedogenic overprint
II-20 surface
c z s g/t
lacustrine

Figure 8. Environmental fluctuations in 'Ubeidiya levels II-21 to II-26, as recorded in Profile 99-A, Trench IIb.

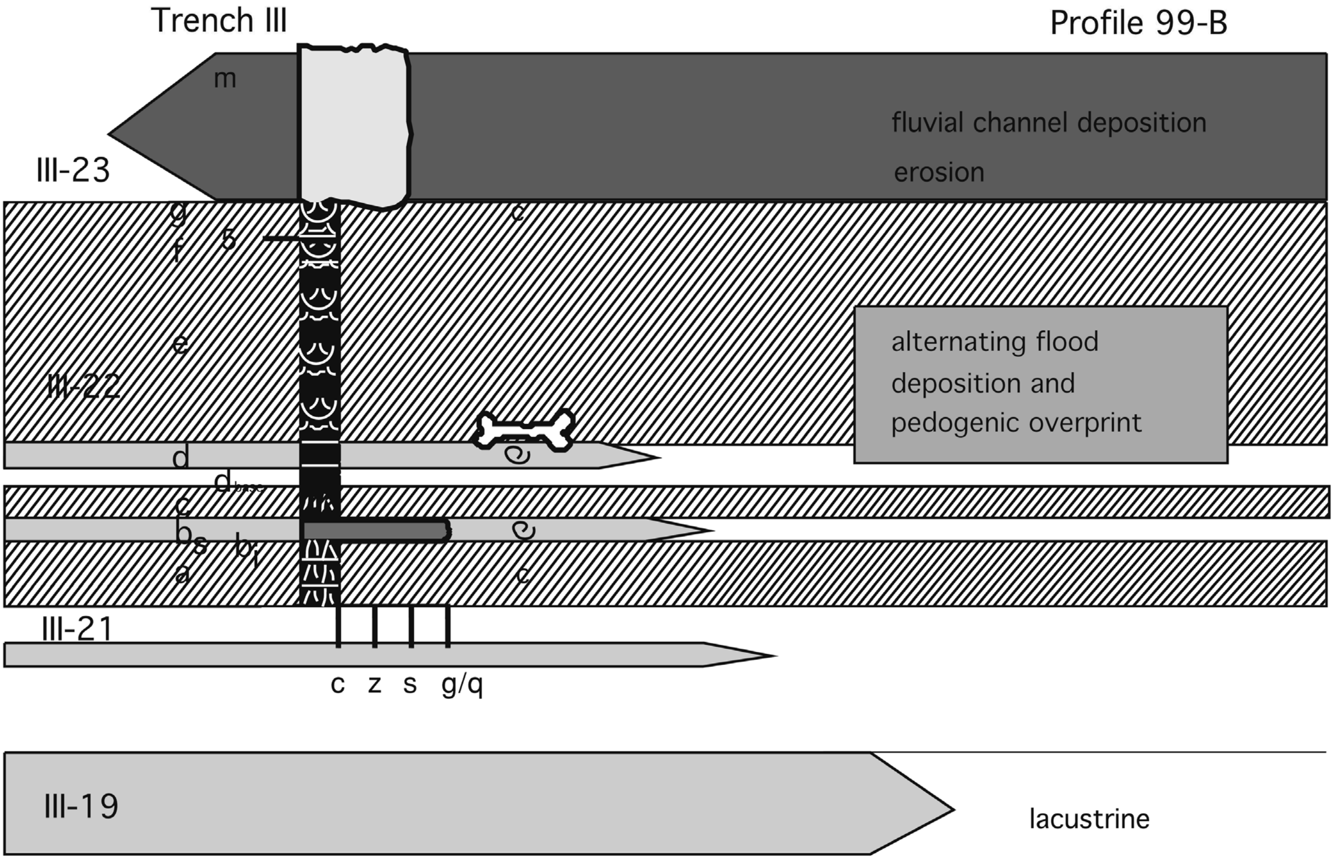
Trench III
Profile 99-B
m
fluvial channel deposition
erosion
III-23
g
f
5
c
e
III-22
alternating flood
deposition and
pedogenic overprint
d
dbase
c
bs
bi
a
c
III-21
c z s g/q
III-19
lacustrine

Figure 9. Environmental fluctuations in 'Ubeidiya levels III-21 to III-23, as recorded in Profile 99-B, Trench III.

The immediate context of both archaeological and faunal accumulations at ʻUbeidiya, as shown above and documented in more detailed analyses (Bar-Yosef & Goren-Inbar 1993; Gaudzinski, this volume), can be constrained to lake-margin settings proper (shorelines), to floodplain settings not far from the shore, and in a few instances (e.g., III-32, -33, -34) to floodplains associated with fluvial channels. The broader context of the archaeological levels is more restricted, occurring only in the Fi Member. Thus, the hominin occupations at ʻUbeidiya reflect a relatively dry phase at the end of the first cycle. Occupations occurred in a variety of settings, but always associated with a proximity to the lake and/or river.

It is difficult to relate the broader setting of the hominin occupations at ʻUbeidiya to a global context, in spite of the age estimate of ca. 1.4 Ma. Without a more precise age determination, or an independent means of estimating the duration of the period of accumulation, detailed correlation is precluded. It is possible to generate a generalized environmental curve, however, which illustrates the structure of long- and short-term variability (Figure 10). Two features are apparent here. First is the two cycles of lake transgression and regression. This most likely reflects climatic control on the basinal hydrographic budget, at one of the dominant Milankovitch periodicities. At ca. 1.4 Ma, the dominant climatic period was the 40 Ka obliquity cycle (deMenocal 1995), and the first-order pattern in the ʻUbeidiya record can be tentatively correlated to such a forcing mechanism. At ca. 1.4 Ma, the positive $\delta^{18}O$ deflection of oxygen isotope stage (OIS) 45

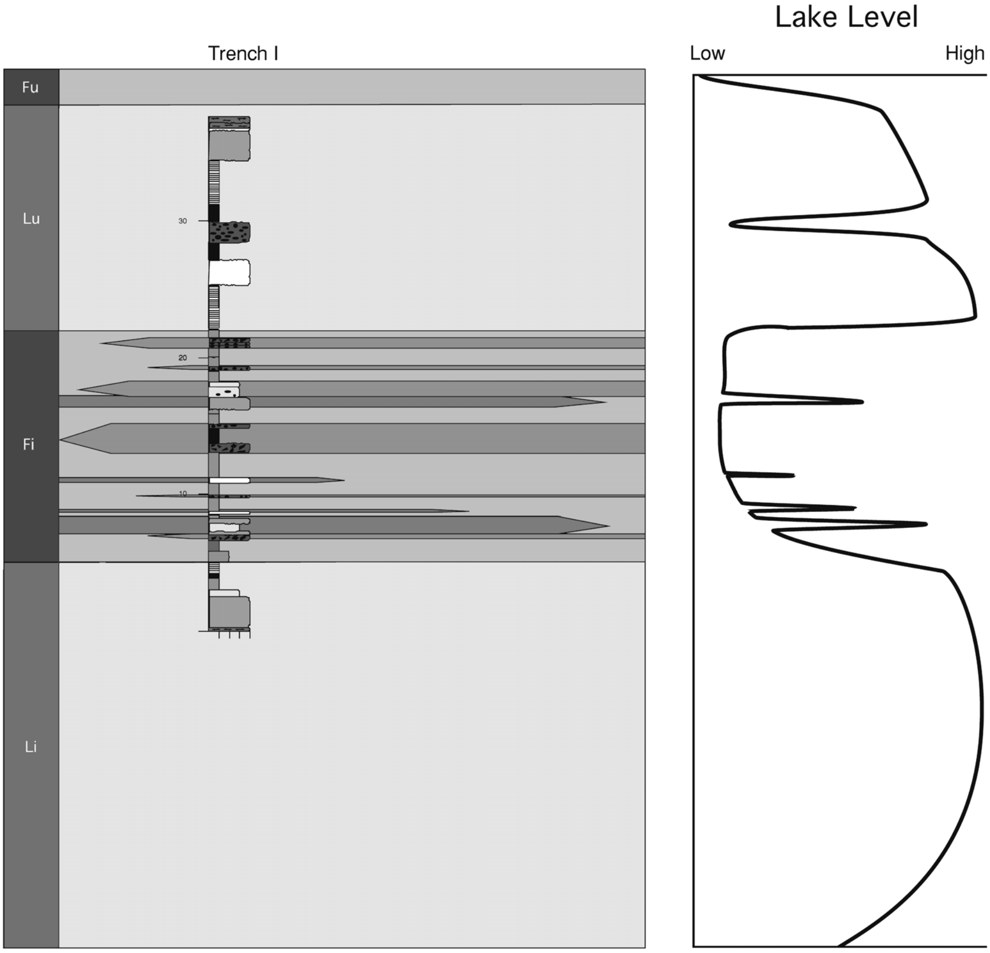

Figure 10. Generalized cyclostratigraphic interpretation of environmental cycles at ʻUbeidiya.

(Shackleton 1995) might account for one of the transgressive (wet) stages of the ʻUbeidiya lake, but the chronometric control on the site is not precise enough to propose a correlation at the present time.

The shorter-term variability shown by the spikes in Figure 10 suggest brief environmental excursions, at the millennial scale or shorter, which had a strong impact on the sedimentary record. This is a characteristic of lake-margin settings, where brief episodes of exposure or drowning are often well preserved in the sedimentary archive. The other aspect of environmental variability mentioned at the beginning of this discussion, recorded in the high degree of lithofacies diversity, indicates a high degree of lateral variability around the site. Rather than a symmetrical pattern of on-lapping and off-lapping marginal facies, environmental shifts were reflected in a wide range of localized habitats shifting across the site. These are primarily based on lacustrine facies, which indicates a wide range of lake habitats associated with the site.

The stratigraphic and sedimentary record of ʻUbeidiya reflects a first-order cyclical pattern of habitat shifts related to fluctuating lake levels, and a secondary variability related to short-term environmental excursions and the local habitat mosaic. Hominins occupied lake-margin (and to a lesser extent stream-margin) settings throughout the complex environmental shifts of the Fi Member. The small area sampled from the ʻUbeidiya Formation is perhaps too limited at this stage to draw any conclusions regarding the lack of evidence from other members, but certainly the hominins repeatedly reoccupied ʻUbeidiya lake margins through considerable environmental variability in Fi Member times.

Constrained cyclicity at Gesher Benot Yaʻaqov

At GBY, wet-site conditions have preserved an unusually rich environmental archive alongside evidence of repeated hominin occupation (Goren-Inbar et al. 2000). The distinctive Acheulian assemblage (Goren-Inbar 1992) occurs alongside evidence for hominin utilization of plant foods (Goren-Inbar et al. 2002), while biotic proxies of environmental parameters range from fossil wood (Werker & Goren-Inbar 2001; Goren-Inbar et al. 2002) to aquatic plants (Melamed 1997) and mammals (Goren-Inbar et al. 2000). The sedimentary record discussed here includes a distinct cyclostratigraphic record which can be magnetostratigraphically calibrated to the marine OIS record of global environmental signals.

The sedimentary sequence at GBY consists of some 35 m of lake margin deposits (Figure 11). The diversity of lithofacies is markedly lower than that seen at ʻUbeidiya. Channel conglomerates bound the sequence at bottom and top. The intervening strata are exclusively lake-margin in character. The strandline is reflected in coquinas and

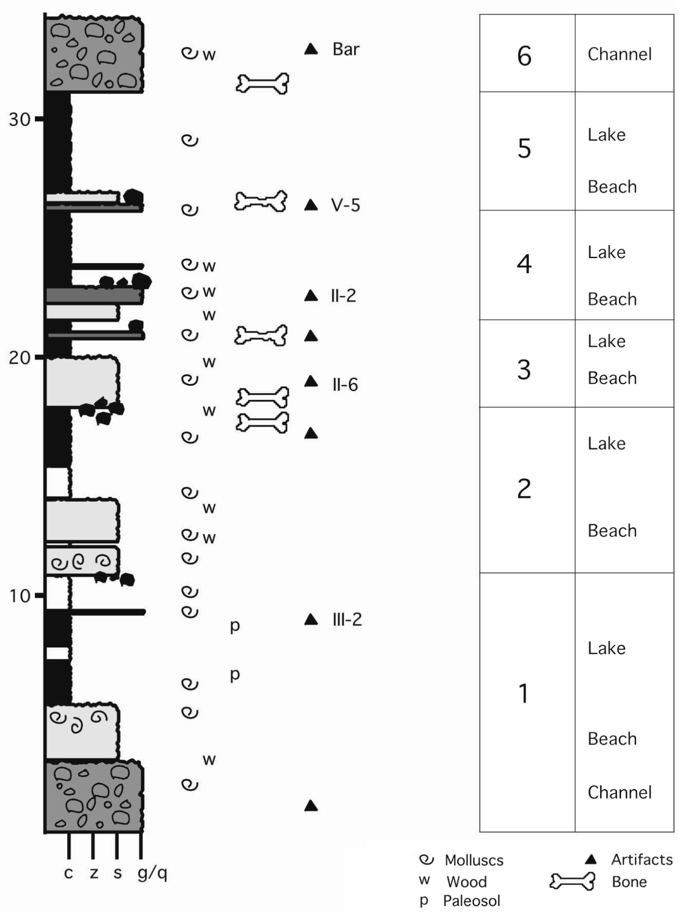

Figure 11. Composite stratigraphic column from Gesher Benot Yaʻaqov, with sedimentary cycles and major depositional environments indicated.

molluscan sands, which preserve the bulk of the archaeological assemblages. Two variants of offshore muds are seen in black (anoxic) and grey (oxic) marls. The offshore facies are overprinted at two levels by pedogenic modification indicating emergence and soil formation.

The stratigraphic sequence at GBY has been interpreted to represent a single first-order cycle, from fluvial conglomerates to lacustrine strata and back, with a series of five second-order cycles nested within, each marked by a shift from marginal to deeper-water facies and back. In diagrammatic form (Figure 12) this cyclical pattern is interpreted to reflect a single first-order climatic cycle at the eccentricity period (ca. 100 Ka), with five nested 20 Ka or precessional cycles within. Interestingly, the two paleosols in the GBY sequence both occur within the first and most prominent wet precessional phase. The interpretation of the GBY cyclostratigraphic pattern in terms of the dominant 100 Ka and nested 20 Ka Milankovitch periods is supported by a variety of sedimentary proxies (especially biofacies), as well as by independent magnetosedimentary properties (Verosub et al. 1998; Goren-Inbar et al. 2000).

A tentative correlation of the GBY cyclostratigraphy to the marine OIS record, tied at the level of the Matuyama-Brunhes Boundary (MBB, 0.78 Ma) magnetic polarity transition (Goren-Inbar et al. 2000), provides a plausible fit of the lake-margin oscillations seen at GBY with the global pattern of climatic variability. The strong transgressive phase of cycle 1 at GBY correlates with the warm/wet peak of OIS 19.3 (and is fixed by the MBB recorded in this cycle).

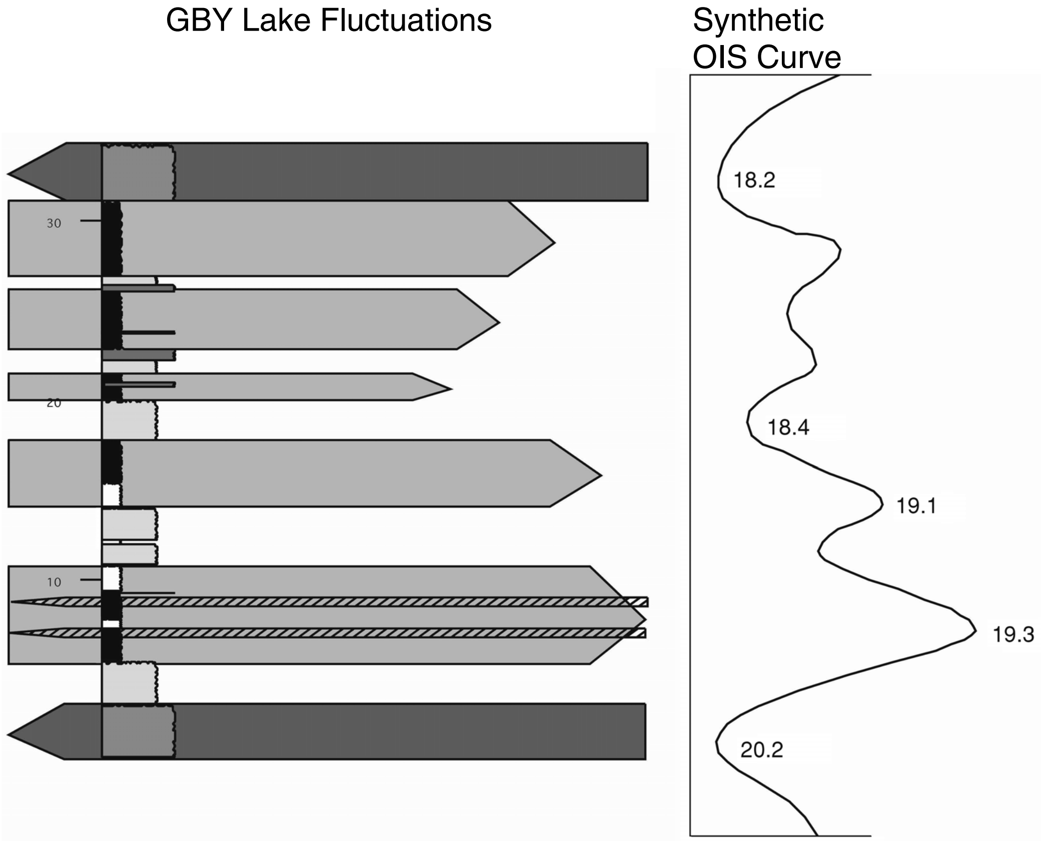

Figure 12. Cyclostratigraphic interpretation of the Gesher Benot Ya'aqov record. A single first-order cycle is apparent from the fluvial-lacustrine-fluvial pattern, while shorter-term oscillations occur within the lacustrine facies. This can be correlated with a synthetic OIS curve (derived from Bassinot et al. 1994 and Tauxe et al. 1996) shown at right based upon the Matuyama-Brunhes Boundary (MBB), the magnetic polarity transition that occurred at 0.78 Ma.

The more moderate transgressive phase of cycle 2 at GBY fits well with the character of OIS 19.1, and the weaker/less coherent patterning of cycles 3, 4 and 5 at GBY fits with the oscillations in OIS 18.3. The bounding conglomerates at the base and top of the sequence are interpreted to reflect the strong cool/dry effects of OIS 20.2 and 18.2, respectively. The two paleosols within the deeper lacustrine phase of cycle 1 again appear to reflect short-term environmental oscillations, of millennial or lesser duration, comparable to those seen at 'Ubeidiya.

The GBY record presents a coherent pattern of environmental oscillations reflecting lake level change and associated habitat and facies shifts. The pattern can be tied to the global OIS proxy record by the MBB, and matched to the cyclostratigraphic record of OIS shifts. The associated hominin record reflects persistent reoccupation of the lake margin setting through a ca. 100 Ka period at the Lower-Middle Pleistocene boundary. The archaeological assemblages derive from three distinct sedimentary contexts (Feibel 2001), indicating that a variety of lake-margin habitats were utilized. The major archaeological levels, including layers II-6 and V-5 (Goren-Inbar et al. 2000) reflect occupations of the shore face, with accumulation on coquinas and molluscan sands. Scattered artifacts were recovered from surfaces on offshore marls, reflecting brief occupation of event (desiccation) surfaces within the marls.

The wide range of climatic oscillations evidenced in the GBY sequence all bear evidence of hominin presence. The cool/dry extremes of OIS 20.2 and 18.2 are reflected in the conglomerates of the section base and top ("the Bar"). Scattered artifacts were recovered (albeit likely transported) from the basal conglomerate, and a rich assemblage was excavated from the Bar (Goren-Inbar et al. 1992). Thus, hominins were on the site, or at least in its vicinity, in the cool/dry extremes of the GBY environmental record. The warm/wet extreme of OIS 19.3 bears the scantest evidence of hominin activity, but this may be more a reflection of the dominance of offshore marls in upper cycle 1. Scattered artifacts were encountered on the surface of one of the paleosols in this cycle, however. It must be noted that a desiccated lake floor would not have the same concentrating effect for hominin activities that would be expected from a strandline, so finding anything at all in this context is quite remarkable. The oscillations of OIS 19.1 and 18.3 have the richest archaeological assemblages, those of layers II-6 and V-5. Again, there may be some facies influence on the absolute abundance of evidence, as these are the best-developed beach complexes of the GBY sequence. With the recognition of variable climatic signatures throughout the GBY sequence, it is now possible to look at the behavioral patterns in the archaeological record in a new light, and perhaps to understand better how these Pleistocene hominins adapted to differing environmental contexts through time.

Patterns of cyclicity in the Pleistocene lakes of the Levant

The record of Levantine lake margins does not stop with GBY, but continues with a wide variety of examples, including the Epipaleolithic occupation at Ohalo II (Kislev et al. 1992), the Natufian site of Eynan (Valla, this volume), and recent adaptations to the Hula swamps and the margins of the Kinneret and Dead Sea. These "younger" occupations have the potential for refined chronological placement (falling within the range of ^{14}C and historical chronologies) and correlation to fine-scale environmental variation and events. At the same time, detailed studies of environmental proxies from the Levant (i.e., Bar-Matthews et al. 1999; Ken-Tor et al. 2001; Bartov et al. 2002) are establishing increasingly detailed histories of environmental context and change, even down to annually resolved records. The potential for correlating behavioral and environmental patterns, and for documenting the ecological context of hominin activities within the Levantine Corridor, is tremendous.

From the oldest sites along the Levantine Corridor, as exemplified by Erq el-Ahmar, 'Ubeidiya, and GBY, we can see that lake margin settings were repeatedly occupied by early hominins, and that they left behind abundant evidence of their activities. The sedimentary record from these sites provides multiple proxies by which we can attempt to reconstruct the character of early environments, along with patterns of change through time. Correlation of these environmental records with the hominin record is heavily dependent upon the richness of the environmental record, along with both the accuracy and precision of correlations by which environmental influences and hominin responses can be tied.

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References

Bar-Matthews, M., Ayalon, A., Kaufman, A. & Wasserburg, G. J. (1999). The Eastern Mediterranean paleoclimate as a reflection of regional events: Soreq cave, Israel. *Earth and Planetary Science Letters* **166**, 85–95.

Bartov, Y., Stein, M., Enzel, Y., Agnon, A. & Reches, Z. (2002). Lake levels and sequence stratigraphy of Lake Lisan, the Late Pleistocene precursor of the Dead Sea. *Quaternary Research* **57**, 9–21.

Bar-Yosef, O. & Goren-Inbar, N. (1993). *The Lithic Assemblages of 'Ubeidiya, a Lower Palaeolithic Site in the Jordan Valley*. QEDEM, Monographs of the Institute of Archaeology 34. Jerusalem: Hebrew University of Jerusalem.

Bassinot, F. C., Labeyrie, L. D., Vincent, E., Quidelleur, X., Shackleton, N. D. & Lancelot, Y. (1994). The astronomical theory of climate and the age of the Brunhes-Matuyama magnetic reversal. *Earth and Planetary Science Letters* **126**, 91–108.

Braun, D., Ron, H. & Marco, S. (1991). Magnetostratigraphy of the hominid tool-bearing Erk el Ahmar Formation in the northern Dead Sea Rift. *Israel Journal of Earth Science* **40**, 191–197.

deMenocal, P. B. (1995). Plio-Pleistocene African climate. *Science* **270**, 53–59.

Feibel, C. S. (2001). Archaeological sediments in lake margin environments. In (J. K. Stein & W. R. Farrand, Eds.) *Sediments in Archaeological Context*. Salt Lake City: University of Utah Press, pp. 127–148.

Goren-Inbar, N. (1992). The Acheulian site of Gesher Benot Ya'aqov: An African or Asian entity? In (Akazawa, T., Aoki, K. & Kimura, T., Eds.) *The Evolution and Dispersal of Modern Humans in Asia*. Tokyo: Hokusen-sha, pp. 67–82.

Goren-Inbar, N., Belitzky, S., Goren, Y., Rabinovich, R. & Saragusti, I. (1992). Gesher Benot Ya'aqov – the "Bar": An Acheulian assemblage. *Geoarchaeology* **7**, 27–40.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–947.

Goren-Inbar, N., Sharon, G., Melamed, Y. & Kislev, M. (2002). Nuts, nut-cracking, and pitted stones at Gesher Benot

Ya'aqov, Israel. *Proceedings of the National Academy of Sciences* **99**, 2455–2460.

Goren-Inbar, N., Werker, E. & Feibel, C. S. (2002). *The Acheulian Site of Gesher Benot Ya'aqov: The Wood Assemblage.* Oxford: Oxbow Press.

Ken-Tor, R., Agnon, A., Enzel, Y., Stein, M., Marco, S. & Negendank, J. F. W. (2001). High-resolution geological record of historic earthquakes in the Dead Sea basin. *Journal of Geophysical Research* **106**(**B2**), 2221–2234.

Kislev, M. E., Nadel, D. & Carmi, I. (1992). Epipalaeolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galilee, Israel. *Review of Palaeobotany and Palynology* **73**, 161–166.

Melamed, Y. (1997). *Reconstruction of the Landscape and the Vegetarian Diet at Gesher Benot Ya'akov Archaeological Site in the Lower Palaeolithic Period*. Unpublished M.S. Thesis, Bar-Ilan University, Ramat Gan, Israel (in Hebrew with English summary).

Ron, H. & Levi, S. (2001). When did hominids first leave Africa? New high-resolution magnetostratigraphy from the Erq-el-Ahmar Formation, Israel. *Geology* **29**, 887–890.

Shackleton. N. J. (1995). New data on the evolution of Pliocene climatic variability. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle, Eds.) *Paleoclimate and Evolution, with Special Emphasis on Human Origins*. New Haven: Yale University Press, pp. 242–248.

Stekelis, M., Picard, L., Schulman, N. & Haas, G. (1960). Villafranchian deposits near 'Ubeidiya in the Central Jordan Valley (Preliminary Report). *Bulletin of the Research Council of Israel* **9G**, 175–183.

Tauxe, L., Herbert, T., Shackleton, N. J. & Kok, Y. S. (1996). Astronomical calibration of the Matuyama-Brunhes boundary: Consequences for magnetic remanence acquisition in marine carbonates and the Asian loess sequences. *Earth and Planetary Science Letters* **140**, 133–146.

Tchernov, E. (1975). *The Early Pleistocene Molluscs of 'Erq el-Ahmar*. Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (1987). The age of the 'Ubeidiya Formation, an Early Pleistocene hominid site in the Jordan Valley, Israel. *Israel Journal of Earth Science* **36**, 3–30.

Tchernov, E. (1999). The earliest hominids in the southern Levant. In (J. Gibert, F. Sánchez, L. Gibert & F. Ribot, Eds.) *The Hominids and Their Environment During the Lower and Middle Pleistocene of Eurasia. Proceedings of the International Conference of Human Palaeontology, Orce, Spain, 1995*. Orce: Museo de Prehistoria y Paleontologia, pp. 389–406.

Werker, E. & Goren-Inbar, N. (2001). Reconstruction of the woody vegetation at the Acheulian site of Gesher Benot Ya'aqov, Dead Sea Rift, Israel. In (B. A. Purdy, Ed.) *Enduring Records, the Environmental and Cultural Heritage of Wetlands*. Oxford: Oxbow Books, pp. 206–213.

Chapter III

Hippos, Pigs, Bovids, Saber-toothed Tigers, Monkeys, and Hominids: Dispersals through the Levantine Corridor during Late Pliocene and Early Pleistocene Times

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Abstract

The Levantine Corridor, bordered on the north by the Taurus-Zagros mountain range, is accepted as the major route out of Africa into Eurasia and vice versa. The facts that the Levant is an extension of the East African Rift and forms an inter-continental bottleneck, and that the climatic and ecological conditions prevailing in East Africa extended north at this time, make the Levant the key area for explaining these dispersal phenomena. This Levantine Corridor has served as a primary dispersal route for Plio-Pleistocene plants and animals. A mixed Ethiopian and Holarctic fauna existed in this region throughout Neogene-Quaternary times. The finding of a group of evolved African taxa in the Early Pleistocene of Eurasia – primates (*Theropithecus oswaldi*), carnivores (*Megantereon whitei*), and ungulates (hippos, pigs, and ruminants) – in connection with the first dispersal of the genus *Homo* to the northern continent reveals a new paleoecological picture of this event.

Introduction

The study of several important Late Pliocene and Early Pleistocene large mammal collections from southern Asia, the Caucasian region, the Middle East, East and North Africa, and southern Europe (see Figure 1) has showed significant faunal connections among them.

The Levantine Corridor is the major route of communication between Africa and Eurasia, and the record in this area shows an important mixed fauna of Holarctic and Ethiopian origin during Late Pliocene and Early Pleistocene times. The species lists of the large mammals from the Late Pliocene site of Bethlehem and the important Early Pleistocene sites of 'Ubeidiya, Evron Quarry, and Gesher Benot Ya'aqov (GBY) provide good examples of an admixed fauna.

On rare occasions during the Late Pliocene and the Early Pleistocene, Ethiopian fauna penetrated north of the Taurus-Zagros mountain range and dispersed toward the Eurasian interior, and Holarctic fauna also penetrated into the African continent.

Late Pliocene

During the Late Pliocene, the record of African fauna in the Levant, at the site of Bethlehem, is marked only by the presence of *Giraffa*, but the finding of African faunal elements in the region of the Caucasus is especially important, specifically at the site of Kuabebi (2.5–2.6 Ma) (Figures 1 and 2). Fossil taxa identified from this site include the procaviid *Kuabebihyrax kachethycus*, the giraffid *Giraffa* sp., the ostrich *Struthio transcaucasicus*, and other African elements (Vekua 1972). This African fauna is partially recorded also in the Balkans and on the Iberian Peninsula, where giraffids have been found in deposits of the Dacic Basin (Romania), in Wolacks (Greece), and recently in the Guadix-Baza Basin (Spain) at the sites of Huélago and Fonelas (Radulesco & Samson 1990; Sickenberg 1967; Alberdi et al. 2000; Arribas et al. 2001). The ostrich *Pachystruthio* sp. has also been found in

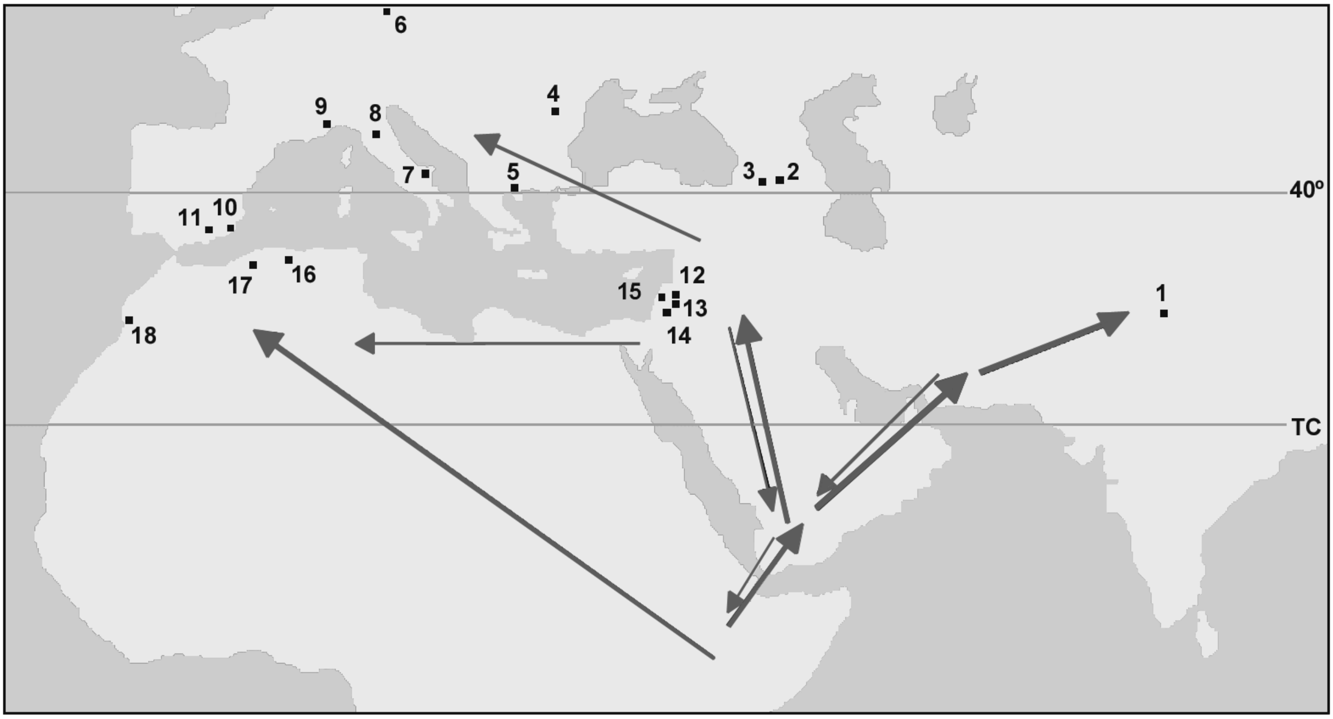

Figure 1. Geographic situation of some of the most important Late Pliocene (LP) and Early Pleistocene (EP) localities of southern and western Asia, Europe and North Africa: 1) Upper Siwaliks (Tatrot: LP; Pinjor: LP+EP; Boulder Conglomerate: EP); 2) Kuabebi: LP; 3) Dmanisi: EP; 4) Dacic Basin: LP+EP; Mygdonia Basin, where the EP site of Apollonia-1 is located together with LP sites; 6) Untermassfeld: EP; 7) Pirro Nord: EP; 8) Upper Valdarno: LP; 9) Vallonet: EP; 10) Cueva Victoria: EP; 11) Guadix-Baza Basin, where the sites of Huélago (LP), Fonelas (LP), Fuente Nueva-1 (LP), Venta Micena (EP), Barranco León (EP) and Fuente Nueva-3 (EP) are located; 12) Gesher Benot Ya'aqov: EP; 13) 'Ubeidiya: EP; 14) Bethlehem: LP; Evron Quarry: EP; 16) Ain Hanech: EP; 17) Ternifine: EP; 18) Ahl al-Oughlam: LP. The arrows mark the possible routes of faunal dispersals.

Romania (Radulesco & Samson 2001). This dispersal event is coincidental with the Eurasian "Elephant-*Equus*" event of Azzaroli et al. (1988). This event marks the appearance in Eurasia of the one-toed horse *Equus stenonis* and *Mammuthus meridionalis*, a modern elephant of African origin (Kalb 1995; Lister & Sher 2001).

In Central and Southern Asia, two dispersal events involving African antelopes have been detected during the Late Pliocene, one at 3.0 Ma and the other at 2.6 Ma. The first (at 3.0 Ma) is marked by the presence of the Hippotragini *Sivotragus brevicornis* (Pilgrim 1939) in the Tatrot Formation of the Upper Siwaliks. The second (at 2.6 Ma) is marked by the presence in the Pinjor Formation, also in the Upper Siwaliks, of the two Hippotragini, *Sivotragus bohlini* and *Oryx sivalensis*, the Reduncini *Vishnocobus patulicornis* and *Sivacobus palaeindicus*, and the Alcelaphini *Damalops palaeindicus* (Pilgrim 1939). The last species was also found in Tajikistan (Dmitrieva 1977).

The Holarctic or Ethiopian origin of the Late Pliocene European and Central Asian large terrestrial Cercopithecidae *Paradolichopithecus* – *P. arvernensis* in Grauceanu (Romania), Vatera (Lesvos Island, Greece), Senèze (France) and La Puebla de Valverde, Cova Bonica, and Moreda (Spain), and *P. sushkini* in Kuruk (Tajikistan) – is controversial. The postcranial anatomy of this genus resembles that of the extant large baboons and suggests an African origin, as was proposed by Mashchenko (1994), but the cranial features are related to those of macaques (Szalay & Delson 1979; Van der Geer & Sondaar 2002), and these data suggest an Holarctic origin.

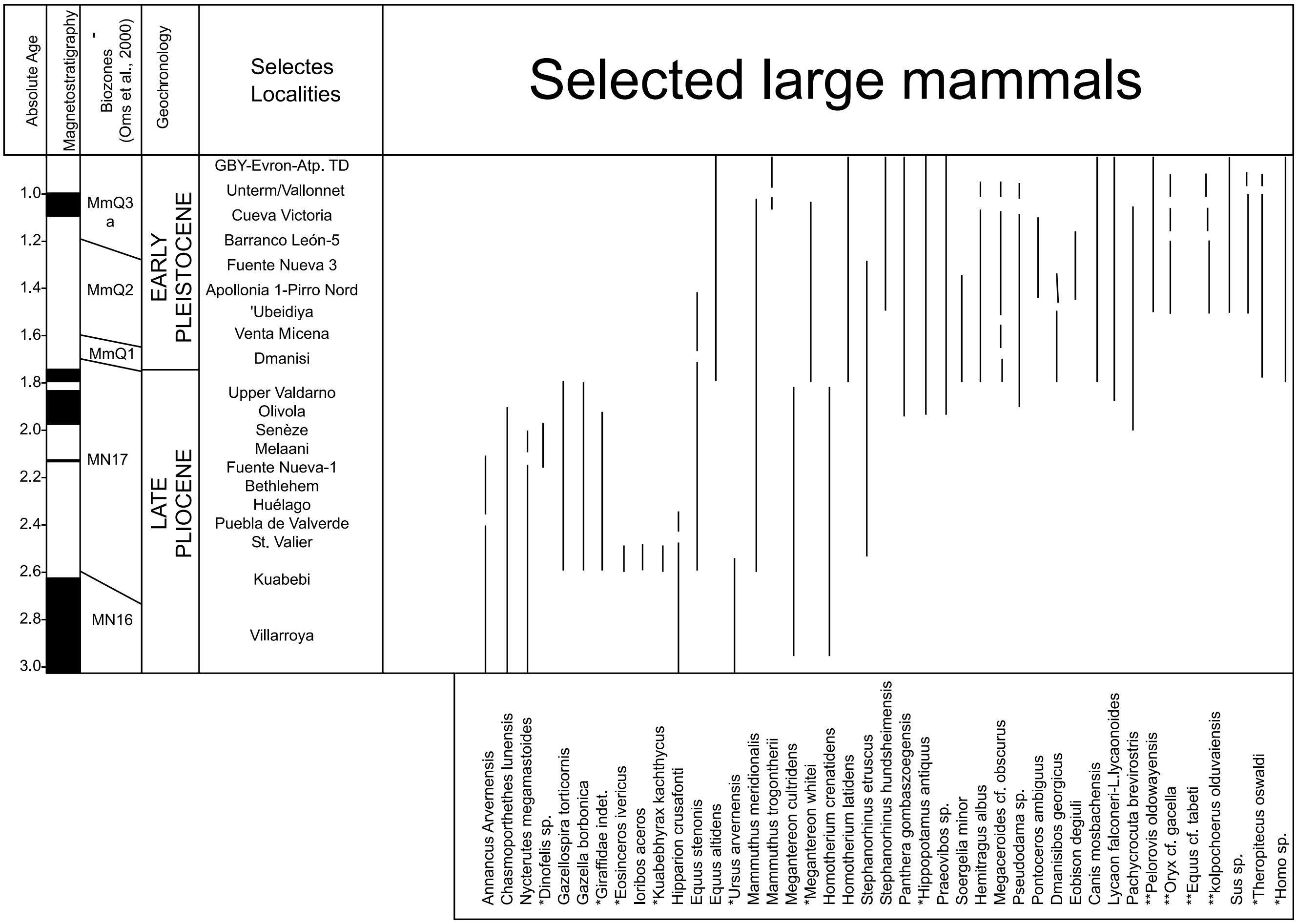

Figure 2. Biostratigraphic chart of selected Late Pliocene and Early Pleistocene large mammals in the Middle East and Europe. The African-origin mammals found only in the Levant are marked by two asterisks, and the African-origin mammals found in several areas of Europe or Asia are marked by one asterisk. The figure shows two important faunal turnovers, one at 2.5 Ma, known in the literature as the "Elephant-*Equus* event" (Azzaroli et al. 1988), and another at the Plio-Pleistocene boundary (at about 1.8 Ma), when hominids arrive in Eurasia at the site of Dmanisi, together with other African-origin species. In the Levant, there appears to be another turnover at 1.4 Ma, the age of ʻUbeidiya, but it could be the result of a gap in the Early Pleistocene record of this area.

Also in the Late Pliocene, important groups of mammals penetrated into Africa. This includes the genus *Equus*, known from the Lake Turkana Basin around 2.3 Ma (Eisenmann 1983; Harris et al. 1988). The route of dispersal may have been the Straits of Bab el-Mandeb, situated at the southern end of the Red Sea (Tchernov 1992; Turner 1999).

In connection with this event, it is important to note that in the late Upper Pliocene deposit of Ahl al-Oughlam in Morocco, there occurs a typical assemblage of large and small African mammals together with two carnivores of Euro-Asiatic origin: the bear *Ursus* cf. *etruscus* and the raccoon dog *Nyctereutes abdeslami* (Geraads 1997). The genera *Ursus* and *Nyctereutes* are well known from Upper Pliocene deposits on the Iberian Peninsula, for example at La Puebla de Valverde (Kurtén & Crusafont 1977). These genera are well known in Asia and *Nyctereutes* is recorded in Bethlehem (Hooijer 1958). The genus *Nyctereutes* (*N. terblanchei*) is also known from South African deposits (Ewer 1956; Ficcarelli et al. 1984). But if the interchange of the above-mentioned fauna across the Levantine Corridor between Eurasia and Africa was made via the Straits of Bab el-Mandeb or the Sinai Peninsula, it is difficult to explain why the genus *Ursus* is not found in other North and East African sites. It is not so preposterous to consider the possibility of selective species interchanges across the Straits of Gibraltar during Late Pliocene times.

The Eurasian-origin Caprini *Capra primaeva* Arambourg (1979) is also found in the Late Pliocene site of Ain Brimba (Tunis).

In this context, the idea that Late Pliocene hominids could have been found outside of Africa in relation to these dispersal events continues to be the subject of lively debate. For the moment, however, no unquestionable Pliocene hominids have been found in Eurasia.

Early Pleistocene

The Plio-Pleistocene transition marks a great change. Hominids arrive in Eurasia together with other endemic African species. This influence of African-origin forms is especially important in the Levant, but some of them have been found in Mirzapur (India), Dmanisi (Georgia), Apollonia (Greece), Orce and Cueva Victoria (Spain), and in other Eurasian assemblages (Table 1, Figures 1 and 2).

As we have seen, the presence of mixed Ethiopian and Holarctic fauna in the Levant is continuous during the Early Pleistocene. Most of the African-origin fauna did not penetrate into northern Eurasia, and most of the Eurasian-origin fauna never penetrated into Africa.

As has been noted previously, the fauna from ‘Ubeidiya is the most diverse example of this blended fauna. The African large mammal species cited at this site are the equid *Equus tabeti* (Eisenmann 1986), the suid *Kolpochoerus olduvaiensis* (Geraads et al. 1986), and the hippopotamid *Hippopotamus gorgops* (Faure 1986), but the main representatives are the ruminants, the giraffid *Giraffa* sp. and the bovids *Oryx* cf. *gazella* and *Pelorovis oldowayensis* (Geraads 1986), the carnivores *Herpestes* sp., *Crocuta crocuta* (Ballesio 1986) and *Megantereon* cf. *whitei* (Martínez-Navarro et al. n.d.), and the cercopithecid primate *Theropithecus* sp. (Belmaker 2002). Most of this fauna, while reaching the Levant, never penetrated north of the Taurus-Zagros Mountains.

Although the finding in the Levant of a large African bovid assemblage in connection with the extension of African environments is very important, none of these elements has been found in other parts of Eurasia. Probably the most significant and best known of these ruminants is the large buffalo *Pelorovis oldowayensis*.

Only a few of the taxa found in ‘Ubeidiya are recorded in other areas of Eurasia: the pig *Kolpochoerus*, the hippo *Hippopotamus* (the species *H. antiquus*), the saber-toothed tiger *Megantereon whitei*, and the monkey *Theropithecus oswaldi*.

In most of Eurasia, the Early Pleistocene assemblages are characterized by the presence of the large supercarrion-eating hyenid *Pachycrocuta brevirostris.* Its first record in Europe is just below the beginning of the Olduvai normal subchron in the Italian Upper Valdarno (Napoleone et al. 2003). It marks the beginning of the Upper Villafranchian in the Olivola Faunal Unit, before the Tasso Faunal Unit. The latter unit is placed just within the upper limit of Olduvai (Torre et al. 1996). The Asian or African origin of *Pachycrocuta brevirostris* is still controversial. Its arrival coincides with the great explosion of the Holarctic *Canis etruscus* on the European continent. *C. etruscus* replaced the raccoon dog *Nyctereutes megamastoides* in the Upper Pliocene. This event is known in the literature as “the wolf event” (Azzaroli et al. 1988), but it would probably be more appropriate to name it “the *Pachycrocuta brevirostris* event,” because of the important record and great impact of this hyenid in most of the Early Pleistocene assemblages of Eurasia (Howell & Petter 1980; Werdelin & Solounias 1991; Turner & Anton 1996).

P. brevirostris is a large hyena, weighing more than 100 kg. It is a non-predatory supercarrion-eating scavenger. In terms of taphonomy, this species is the most important agent of fossil accumulation at Early Pleistocene sites in Europe, e.g., Venta Micena in Spain (Palmqvist et al. 1996; Arribas & Palmqvist 1998; Martínez-Navarro & Palmqvist 1999; Palmqvist & Arribas 2001).

Table 1. Large mammal faunal lists of the Early Pleistocene sites of Gesher Benot Ya'aqov, Israel (Hooijer 1959, 1960; Geraads & Tchernov 1983; Goren-Inbar et al. 2000; Martínez-Navarro et al. 2000); 'Ubeidiya, Israel (Tchernov 1986; Martínez-Navarro et al. n.d.); Dmanisi, Georgia (Vekua 1995; Martínez-Navarro & Palmqvist 1995; and pers. obs.); Venta Micena, Spain (Moyà-Solà et al. 1987; Martínez-Navarro 1991; Martínez-Navarro & Palmqvist 1995; Eisenmann 1999; Cregut-Bonnoure 1999; Martínez-Navarro & Rook n.d.); and Ain Hanech, Algeria (Arambourg 1979; Sahnouni & de Heinzelin 1998; and pers. obs.). The African-origin species are marked with an asterisk. In Europe the Holarctic fauna is dominant and only few taxa of African origin are present. In North Africa, the Ethiopian fauna is dominant and only a few Holarctic taxa are present. In the Middle East, especially at 'Ubeidiya, Holarctic and Ethiopian faunas are mixed and well represented. _Homo_ sp. at Ain Hanech is documented only by the presence of lithic artifacts.

Gesher Benot Ya'aqov	**'Ubeidiya**	**Dmanisi**	**Venta Micena**	**Ain Hanech**
Primates:	**Primates:**	**Primates:**	**Primates:**	**Primates:**
*_Homo_ sp.	_Macaca silvana_	*_Homo_ cf. _ergaster_		*_Homo_ sp.
	*_Theropithecus_ sp.			
	*_Homo_ sp.			
Carnivora:	**Carnívora:**	**Carnívora:**	**Carnívora:**	**Carnivora:**
Ursus sp.	_Ursus etruscus_	_Ursus etruscus_	_Ursus etruscus_	
Felidae indet. (large size)	_Canis mosbachensis_	_Ursus_ sp.		
	Lycaon lycaonoides	_Canis etruscus_	_Canis mosbachensis_	
	Vulpes sp.		_Lycaon lycaonoides_	_Lycaon lycaonoides_
	Lutra sp.		_Vulpes praeglacialis_	
	Pannonictis ardea		Cf. _Meles_ sp.	
	Vormela cf. _peregusna_	_Homotherium_ sp.		
Hyenidae indet.	*_Megantereon_ cf. _whitei_	*_Megantereon whitei_	_Homotherium_ sp.	
	Lynx sp.	_Panthera gombaszogensis_	*_Megantereon whitei_	
	Felis sp. (taille chaus)		_Lynx_ sp.	
	*_Crocuta crocuta_			
	*_Herpestes_ sp.	_Pachycrocuta brevirostris_	_Pachycrocuta brevirostris_	*_Crocuta crocuta_
Artiodactyla:	**Artiodactyla:**	**Artiodactyla:**	**Artiodactyla:**	**Artiodactyla:**
Sus cf. _scrofa_	*_Kolpochoerus olduvaiensis_			*_Kolpochoe. phacochoeroides_
*_Hippopotamus amphibius_	_Sus_ sp.		*_Hippopotamus antiquus_	*_Hippopotamus amphibius_
	*_Hippopotamus behemoth_			
	*_Hippopotamus gorgops_			
	Camelus sp.			*_Sivatherium maurasium_
	*Giraffidae gen. indet.	*_Paleotragus_ indet.		*_Giraffa pomeli_
Megaloceros sp.	_Praemegaceros verticornis_	_Eucladoceros senezensis_	_Megaceroides_ sp.	
Dama cf. _mesopotamica_	Cervidae gen. et sp. indet.	_Pseudodama nestii_	_Pseudodama_ sp.	*_Pelorovis bubaloides_
Cervus cf. _elaphus_	*_Pelorovis oldowayensis_	_Cervus perrieri_	Bovini gen. et sp. indet. 1	_Bos praeafricanus_
Bovini indet. (cf. _Bison_ sp.)	Bovini indet. (cf. _Bison_ sp.)	Bovini gen. et sp. indet.	Bovini gen. et sp. indet. 2	*_Oryx_ sp. cf. _Oryx gazella_
*_Pelorovis_ cf. _bubaloides_	*_Oryx_ sp. cf. _Oryx gazella_	_Dmanisibos georgicus_	_Soergelia minor_	*_Alcelaphus_ sp.
Ovibovini indet.	*Hippotragini indet.		_Praeovibos_ sp.	*_Gorgon mediterraneus_
Gazella sp.	_Gazella_ sp.	_Soergelia_ sp.		*_Taurotragus gaudryi_
Caprini indet.	Antilop. indet. (cf. _Spirocerus_ sp.	Antilopini indet.	Antilopini indet.	*_Gazella pomeli_
	or _Pontoceros_ sp.)	Caprini indet. cf. _H. albus_	_Hemitragus albus_	*Hippotragini indet.
Perissodactyla:	**Perissodactyla:**	**Perissodactyla:**	**Perissodactyla:**	**Perissodactyla:**
Equus cf. _caballus_	Stephanorhinus etruscus etruscus	_Stephanorhinus etruscus_	_Stephanorhinus etruscus_	*_Ceratotherium simum_
Stephanorhinus merckii	*_Equus_ cf. _tabeti_	_Equus_ sp. aff. _E. altidens_		*_Hipparion libycum_
	Equus cf. _caballus_	_Equus_ cf. _stenonis_	_Equus granatensis_	*_Equus tabeti_
Proboscidea:	**Proboscidea:**	**Proboscidea:**	**Proboscidea:**	**Proboscidea:**
Stegodon mediterraneus	_Mammuthus meridionalis_	_Mammuthus meridionalis_	_Mammuthus meridionalis_	_Mammuthus meridionalis_
Paleoloxodon antiquus				
		Aves:		**Aves:**
		*_Struthio dmanisensis_		_Struthio barbarus_

The most important faunal change in Europe and western Asia lies just after the Tasso Faunal Unit, with almost complete replacement of ungulates and carnivores. The paradigmatic site where this change has been detected is Dmanisi in Georgia (Vekua 1995), dated 1.81 Ma (Lumley et al. 2002), but it is also recorded in many other sites in Europe and western Asia.

The significant taxa

Pelorovis

Pelorovis, which evolved from the early Pliocene *Simatherium* (Vrba 1987), is the large Late Pliocene and Pleistocene buffalo from Africa. It is a common bovid in the savannas of this continent until the extinction of its last representative species, *Pelorovis antiquus*, in the Upper Pleistocene.

Pelorovis was unknown outside of Africa until the first record in the Levant at the site of 'Ubeidiya, where a large skull of *Pelorovis oldowayensis*, the species from Olduvai, was found (Geraads 1986). This taxon is very well known in most of the Late Pliocene and Early Pleistocene East African assemblages. In the most recent field seasons at 'Ubeidiya, new material of *Pelorovis* has been uncovered. In addition, a form of *Pelorovis* has recently been described at GBY (Martínez-Navarro et al. 2000). It is represented by a skull from the old collections and several teeth and postcranial elements from the new collections excavated by Naama Goren-Inbar.

At present, it is unknown whether the form of *Pelorovis* from GBY is an endemic form evolved in the Levant or corresponds to a new arrival from Africa. In any case, it is the species of *Pelorovis* found at the Early Pleistocene North African site of Ain Hanech (Algeria), described as *Bos bubaloides* (Arambourg 1979), and this form is also similar to *Pelorovis turkanensis* described at Koobi Fora and West Turkana in East Africa (Harris 1991).

A form of *Pelorovis* (*P*. cf. *oldowayensis*) is also cited at the Early Pleistocene deposits of the An Fafud desert in the north of Saudi Arabia (Thomas et al. 1998).

Actually, *Pelorovis* has never been found outside of the Levant, but its arrival in this region of western Asia, together with other African ruminants of open environments, suggests the extension of the African savannas into the middle latitudes during Early Pleistocene times.

Kolpochoerus

A significant finding in the Levant is the presence of African pigs, specifically the genus *Kolpochoerus*, the ancestor of the extant *Hylochoerus*, the forest hog. It is found in 'Ubeidiya, where it is cited as *K. olduvaiensis* (Geraads et al. 1986), and in Evron Quarry, cited as *K. evronensis* (Tchernov et al. 1994). In North Africa, this genus is well known and cited as *K. phacochoeroides* in several sites, including Ain Hanech and Ahl al-Oughlam (Geraads 1993).

The genus *Metridichoerus*, ancestor of the warthog *Phacochoerus*, is also cited in North Africa, at the late Early Pleistocene site of Ternifine in Algeria. The specimens from Evron were previously ascribed to *Metridichoerus* (Haas 1970).

The African suids are basically characterized by the development of the cigomatic arch and the development of a large complex talonid in the third molars, with several pairs of cuspids. The enamel is also very thick. Recent reinterpretation of published material concludes that *Kolpochoerus* is found in other Asian Early Pleistocene sites (Martínez-Navarro & Shabel n.d.). The genus *Kolpochoerus* has been interpreted as an evolved African form from an Asian immigrant during the Middle Pliocene (Harris & White 1979; Harris 1983; Pickford 1994). The oldest recognized species of the genus was previously *K. afarensis* from Hadar (Cooke 1978), but a new study of the Early and Middle Pliocene suid material from Ethiopia and Chad has determined the presence of a primitive species that gave rise to the *Kolpochoerus* lineage in the African continent, *K. deheinzelini* (Brunet & White 2000). It evolved from the Late Miocene Asian species *Propotamochoerus hysudricus*.

The evolution of *K. deheinzelini* gave rise to *K. cookei*, a small-sized and hypsodont species that is only found in

Hadar, and to *K. afarensis*, which gave rise to *K. majus* and to *K. limnetes-K. olduvaiensis* (Brunet & White 2000). The last representatives of *Kolpochoerus* in Africa are *K. olduvaiensis* in Olduvai Bed IV, Tanzania (0.78 Ma) and *K. majus* in Bodo, Middle Awash, Ethiopia (0.6 Ma) (White 1995). In the Early Pleistocene an evolved form of *Kolpochoerus limnetes* dispersed into Asia, probably following the expansion of gallery forest into the middle latitudes.

Hippopotamus

Although the species represented in 'Ubeidiya are the African form *Hippopotamus gorgops* and the endemic species *H. behemoth* (Faure 1986), in areas north of the Taurus-Zagros mountain range the only recorded species of this genus during the Early Pleistocene is *Hippopotamus antiquus*, related to the extant *Hippopotamus amphibius*.

At the time of the Plio-Pleistocene boundary, this African megaherbivore, *H. antiquus*, penetrated into Eurasia. The record of this species was published in the Upper Valdarno at the Tasso Faunal Unit (Gliozzi et al. 1997), although a new reinterpretation of this finding suggests that the hippopotamus described by Nesti at the beginning of the nineteenth century was found in younger deposits (Napoleone et al. 2003). Then, the oldest record of this species in Europe is found at the site of Venta Micena in Spain at around 1.5 Ma (Alberdi & Ruiz-Bustos 1985). Later, this species is found in most of the European and western Asian Early Pleistocene faunal assemblages until the cold climatic change that begins the Middle Pleistocene.

The movements of the hippos are different from the other terrestrial large mammals because of the amphibious behavior of these animals and their ability to cross long stretches of water.

Megantereon whitei

A study of the fauna from Venta Micena (Martínez-Navarro 1991, 1992a, b) revealed the presence of a saber-toothed tiger of African origin belonging to the genus *Megantereon*, and differing from the Late Pliocene Eurasian form *Megantereon cultridens*. The specimens from Venta Micena were classified as *M. whitei* and this species was also noted at Dmanisi at the other longitudinal limit of the Mediterranean Basin (Martínez-Navarro & Palmqvist 1995). *M. whitei* has also been documented at the Greek site of Apollonia-1 (Martínez-Navarro & Palmqvist 1996), and it is probably present at Untermassfeld (Germany), where it has been classified as *Megantereon cultridens adroveri* (Hemmer 2001), a synonym of *M. whitei* (Martínez-Navarro & Palmqvist 1995). A form of *Megantereon* is also recorded at 'Ubeidiya (Ballesio 1986; Martínez-Navarro et al. n.d.), as well as in extreme southeast Asia, in Java (Indonesia) (Kurtén 1962; De Vos & Aziz 1987), together with *Pachycrocuta brevirostris* (Geraads 1979).

The origin of the genus *Megantereon* is controversial. Berta & Galiano (1983) proposed an Early Pliocene North American origin. Werdelin & Lewis (2000, 2002) described a new species, *Megantereon ekidolt*, dating to 3.5 Ma from the South Turkwell hominid site in the Turkana Basin. This species is a primitive form in the lineage of *M. whitei* (Palmqvist 2002) and differs from the Eurasian Upper Pliocene form *Meganteron cultridens*, for which the oldest record in Europe is at the site of Villarroya (Spain) at around 3.0 Ma. At the Plio-Pleistocene boundary, *M. whitei* replaced *M. cultridens* in Eurasia (Martínez-Navarro & Palmqvist 1995).

The principal differences between *M. whitei* and *M. cultridens* are the reduction of the premolar series and the presence of a proportionally longer canine in the African species. In general aspects, *M. whitei* is a more specialized hypercarnivorous predator than *Megantereon cultridens*.

Together with *Hippopotamus antiquus*, *M. whitei* is the best-known species of African origin from the Eurasian Early Pleistocene. It is found in the eastern and western northern Mediterranean areas together with the earliest evidence of human presence outside of Africa (Bar-Yosef & Goren-Inbar 1993; Martínez-Navarro et al. 1997; Oms et al. 2000; Gabunia et al. 2000; Vekua et al. 2002; Belmaker et al. 2002). In East and South Africa, *M. whitei* is also commonly found in association with hominids in Late Pliocene and Early Pleistocene sites (Leakey 1976; Howell &

Petter 1976; Turner 1987; Martínez-Navarro & Palmqvist 1995).

The African and Eurasian record of *M. whitei* shows that this species evolved in Africa during the Late Pliocene and dispersed at the Plio-Pleistocene boundary into Eurasia through the Levantine Corridor. Its last record is around 1.0 Ma in Europe and Africa at the sites of Untermassfeld and Swartkrans, respectively. This species was a super-predator felid which inhabited mixed habitats.

Theropithecus oswaldi

Fossil teeth of the large-sized African cercopithecid *Theropithecus* cf. *oswaldi* were uncovered in association with *P. brevirostris* at the karstic site of Cueva Victoria in Cartagena, southeast Spain (Gibert et al. 1995) (dated approx. 1.0 Ma). This is the only published finding of this theropithecine species in Europe, although there is another record in Asia at the late Lower Pleistocene site of Mirzapur (India), situated in the Lower Boulder Conglomerate (Gupta & Sahni 1981; Delson 1993; Pickford 1993) and also dated by paleomagnetism at 1.0 Ma (Azzaroli & Napoleone 1980). The presence of *Theropithecus* in the Early Pleistocene of the Levant is now becoming well documented as well, based upon its recent finding at the site of 'Ubeidiya (Belmaker 2002). This last finding shows a clear dispersal of this species through the Levantine Corridor.

This large monkey, *Theropithecus oswaldi,* is also found in the late Early Pleistocene North African site of Ternifine (Delson & Hoffstetter 1993). But this genus of cercopithecid is well known from the beginning of the Pliocene in the majority of African faunal assemblages associated with hominids. Both *Theropithecus* and hominids have their origin in East Africa, and their evolution and dispersal are parallel until the Middle Pleistocene (Pickford 1993), when *Theropithecus* became restricted to a single species of small size, *T. gelada*, that now only survives in the mountains of Ethiopia. *Theropithecus oswaldi* evolved from *T. darti*, and the members of this lineage are commonly found in African assemblages from the beginning of the Late Pliocene (3.3 Ma) until the Middle Pleistocene (0.5 Ma; Delson 1993; Leakey 1993; Pickford 1993). In the Late Pliocene a smaller species of theropithecine monkey (*Theropithecus atlanticus*) is known in North Africa, where it is well documented at the interesting site of Ahl al-Oughlam (Casablanca, Morocco; (Alemseged & Geraads 1998). *T. atlanticus* is an evolved branch of *T. darti*, and it is apparently a North African species from the end of the Pliocene.

Early Pleistocene Eurasian species in North Africa

A few large mammal species of Eurasian origin penetrated into Africa during the Early Pleistocene, especially into the north. An example is the elephant *Mammuthus meridionalis,* recorded at Ain Hanech; this species of African origin colonized Eurasia during the Late Pliocene and returned to North Africa during the Early Pleistocene (Sahnouni & de Heinzelin 1998).

Another example of considerable interest is the entrance into Africa, at the beginning of the Early Pleistocene, of the widely distributed Holarctic carnivore *Canis* (*Xenocyon*) ex. gr. *falconeri* (Rook 1994), synonym of *Lycaon lycaonoides* (Martínez-Navarro & Rook n.d.), the ancestor of the extant tetradactyl wild dog *Lycaon pictus*. *L. lycaonoides* is known in Ain Hanech, where it has been referred to *Canis atrox* (Arambourg 1979), but also in the east and the south of the continent, including Olduvai Beds I and II (Ewer 1965), and Kromdraai A (Turner 1986).

Discussion

On the basis of this study, it is possible to see the great confusion that exists with regard to the systematics of the Late Pliocene and Early Pleistocene large mammals from Eurasia, the Middle East, and North Africa. Direct study of the collections has revealed a large number of existing synonyms (see Table 1, which presents the large mammal lists from the Early Pleistocene sites of GBY, 'Ubeidiya, Dmanisi, Venta Micena, and Ain Hanech).

In Dmanisi, Venta Micena, Cueva Victoria, and other European deposits such as Pirro Nord in Italy (De Giuli et al. 1987), Apollonia in Greece (Koufos & Kostopoulos 1997; Kostopoulos 1997), and Untermassfeld in Germany (Kahlke 1997, 2001a, b), the dominant type of fauna is Holarctic; in North Africa, the dominant fauna is Ethiopian; and in the Near East, both faunal types are present. In the map shown in Figure 1, it is possible to see and understand that the majority of these faunal dispersals have occurred via the Levantine Corridor.

The biostratigraphical chart of selected large mammals in Europe and the Near East (Figure 2) shows the relative age of some of the most important sites of these regions. The figure shows the important replacement of fauna at the Plio-Pleistocene boundary at more or less the same time that hominids arrived in Eurasia. Most of these new species in Europe have an Holarctic origin, and some of them arrived from Africa, although most of the latter never crossed the Taurus-Zagros Mountains and are only recorded in the Levantine area, like *Equus* cf. *tabeti*, *Pelorovis oldowayensis*, *Oryx* cf. *gazella*, and other ruminants.

White (1995) related the evolution of African omnivores to global climatic changes, based on the timing of the first and last appearance data of the different hominid and suid species. The genus *Theropithecus* must be included in this group, as it is also found in most of the African Plio-Pleistocene assemblages with hominids and suids (Pickford 1993). Hominids, *Theropithecus*, and suids have parallel evolutionary histories in Africa but, in light of the finding of *Theropithecus* in the Middle East, India, and Spain, and given the discovery of *Kolpochoerus* in the Middle East and probably in other areas of Asia as well (Martínez-Navarro & Shabel n.d.), we must suppose that they also have parallel dispersals during the Early Pleistocene.

The Early Pleistocene dispersal of fauna and hominids out of Africa is related to changes in climate and to modes of food resource exploitation as well. Late Pliocene African hominids are characterized by an increase in the thickness of their enamel which appears after the change of ecological conditions toward greater aridity at 2.5 Ma (Ramirez-Rozzi et al. 1999). The change in enamel thickness probably reflects an adaptation to more fibrous and abrasive plant foods.

A similar and parallel process of enamel thickness increase is detected in the genera *Theropithecus* and *Kolpochoerus*, i.e., 1.5 mm thick for the East African molar specimens of *T. oswaldi* (Benefit 1999) and 2.7 mm thick for the M_3 of *Kolpochoerus* from Evron Quarry, Israel. Related to the same phenomena, an important increase in the size of the third molar is also detected in *Kolpochoerus* (Harris & White 1979).

At the Early/Middle Pleistocene Acheulian site of GBY (0.7–0.8 Ma BP), the exploitation of acorns, chestnuts, and other nuts by hominids has recently been documented (Goren-Inbar et al. 2002). These foods could typically have been eaten by other omnivores, like pigs (e.g., *Kolpochoerus*) and large monkeys (e.g., *Theropithecus*).

In clear competition with hyenas, especially the large *Pachycrocuta brevirostris*, another classical resource for hominids is carrion, most of it left by large carnivores, especially *Megantereon whitei*, a non-cursorial flesh-eater adapted to mixed habitats. This saber-toothed tiger has elongated and non-crenulated upper canines, a short mandible, and powerful forelimbs. It is well adapted to hunting but its masticator structure only allows it to eat the soft parts of its prey, leaving most of the carcasses intact (Martínez-Navarro & Palmqvist 1996). Other flesh-eaters and non-bone-cracking predators, like *Lycaon lycaonoides* or *Homotherium latidens*, could also be part of this scenario, producing partial carcasses for scavenging.

Theropithecus or *Kolpochoerus* could also have been opportunistic scavengers, but this is unlikely to have been a systematic behavior in these species as it was in *Pachycrocuta brevirostris* and perhaps in *Homo*.

Conclusions

At the Plio-Pleistocene boundary, hominids arrived into Eurasia following the route of the Levantine Corridor. This out-of-Africa dispersal of the genus *Homo* is related to general ecological conditions that permitted the dispersal of other large mammals, particularly *Kolpochoerus limnetes*, *Megantereon whitei* and *Theropithecus oswaldi*, which was favored by the northward expansion of African mixed habitats – savannas and gallery forest – and their particular patterns of foraging

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References

Alberdi, M. T., Alonso, M. A., Azanza, B., Hoyos, M. & Morales, J. (2001). Vertebrate taphonomy in circum-lake environments: Three cases in the Guadix-Baza Basin (Granada, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **165**, 1–26.

Alberdi, M. T. & Ruiz-Bustos, A. (1985). Descripción y significado bioestratigráfico del *Equus* e Hipopótamo en el yacimiento de Venta Micena (Granada). *Estudios Geológicos* **41**, 251–261.

Alemseged, Z. & Geraads, D. (1998). *Theropithecus atlanticus* (Thomas, 1884) (Primates: Cercopithecidae) from the Late Pliocene of Ahl al Oughlam, Casablanca, Morocco. *Journal of Human Evolution* **34**, 609–621.

Arambourg, C. (1979). *Vertebres Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux)*. Paris: Singer-Polignac.

Arribas, A. & Palmqvist, P. (1998). Taphonomy and palaeoecology of an assemblage of large mammals: Hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios* **31**, 3–47.

Arribas, A., Riquelme, J. A., Palmqvist, P., Garrido, G., Hernández, R., Laplana, C., Soria, J. M., Viseras, C., Durán, J. J., Gumiel, P., Robles, F., López-Martínez, J. & Carrión, J. (2001). Un nuevo yacimiento de grandes mamíferos villafranquienses en la cuenca de Guadix-Baza (Granada): Fonelas P-1, primer registro de una fauna próxima al límite Plio-Pleistoceno en la Península Ibérica. *Boletín Geológico y Minero* **112**, 3–34.

Azzaroli, A., De Giuli, C., Ficcarelli, G. & Torre, D. (1988). Late Pliocene to early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events. *Palaeogeography, Palaeoclimatology, Palaeoecology* **66**, 77–100.

Ballesio, R. (1986). Les carnivores du Pléistocène d'Oubeidiyeh (Israël). In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jordain à Oubeidiyeh*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem **5**, pp. 63–92.

Bar-Yosef, O. & Goren-Inbar, N. (1993). *The Lithic Assemblage of ʻUbeidiya. A Lower Paleolithic Site in the Jordan Valley*. Qedem 34, Monographs of the Institute of Archaeology. Jerusalem: Hebrew University of Jerusalem, pp. 1–266.

Belmaker, M. (2002). First evidence of the presence of *Theropithecus* sp. in the Southern Levant. *Israel Journal of Zoology* **48**, 165.

Belmaker, M., Tchernov, E., Condemi, S. & Bar-Yosef, O. (2002). New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *Journal of Human Evolution* **43**, 43–56.

Benefit, B. R. (1999). Biogeography, dietary specialization, and the diversification of African Plio-Pleistocene monkeys. In (T. G. Bromage & F. Schrenk, Eds.) *African Biogeography,* *Climate Change, and Human Evolution*. Oxford: Oxford University Press, pp. 172–188.

Berta, A. & Galiano, H. (1983). *Megantereon hesperus* from the late Hemphillian of Florida with remarks on the phylogenetic relationship of machairodonts (Mammalia, Felidae, Machairodontinae). *Journal of Paleontology* **57**, 892–899.

Brunet, M. & White, T. D. (2000). Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Éthiopie; Tchad). *Comptes Rendus Academie des Sciences, Paris* **332**, 51–57.

Cooke, H. B. S. (1978). Pliocene-Pleistocene Suidae from Hadar, Ethiopia. *Kirtlandia* **29**, 1–63.

Cregut-Bonnoire, E. (1999). Les petits Bovidae de Venta Micena (Andolousie) et de Cueva Victoria (Murcia). In (J. Gibert, F. Sánchez, L. Gibert & F. Ribot, Eds.) *The Hominids and their Environment during the Lower and Middle Pleistocene of Eurasia. Proceedings of the International Conference of Human Paleontology, Orce 1995*, pp. 191–228.

De Giuli C., Masini, F. & Torre, D. (1987). The latest Villafranchian faunas in Italy: The Pirro Nord fauna (Apricena, Gargano). *Palaeontographia Italica* **74**, 51–62.

Delson, E. (1993). *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In (N. G. Jablonski, Ed.) *Theropithecus: The Rise and Fall of a Primate Genus*. Cambridge: Cambridge University Press, pp. 157–189.

Delson, E. & Hoffstetter, R. (1993). *Theropithecus* from Ternifine, Algeria. In (N. G. Jablonski, Ed.) *Theropithecus: The Rise and Fall of a Primate Genus.* Cambridge: Cambridge University Press, pp. 191–208.

De Vos, J. & Aziz, F. (1987). Note on two upper canines of *Megantereon* sp. (Mammalia, Felidae) from the Pleistocene of Java. *Proceedings* **B90**, 57–63.

Dmitrieva, E. L. (1977). Tajikistan's and India's fossil Alcelaphinae. *Journal of the Palaeontological Society of India* **20**, 97–101.

Eisenmann, V. (1983). Family Equidae. In (J. M. Harris, Ed.) *Koobi Fora Research Project 2: The Fossil Ungulates: Proboscidea, Perissodactyla and Suidae.* Oxford: Clarendon Press, pp. 156–214.

Eisenmann, V. (1986). Les Equidés du Pléistocène d'Oubeidiyeh. In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jordain à Oubeidiyeh*, Mémoires et Travaux du Centre de Recherche Français de Jérusalem **5**, pp. 191–212.

Eisenmann, V. (1999). *Equus granatensis* of Venta Micena and evidence for primitive non-stenonid horses in the Lower Pleistocene. In (J. Gibert, F. Sánchez, L. Gibert & F. Ribot, Eds.) *The Hominids and their Environment during the Lower and Middle Pleistocene of Eurasia. Proceedings of the International Conference of Human Paleontology, Orce 1995*, pp. 175–190.

Ewer, R. F. (1956). The fossil carnivores of the Transvaal caves: Canidae. *Proceedings of the Zoological Society of London* **126**, 97–119.

Ewer, R. F. (1965). Large carnivora. In (L. S. B. Leakey, Ed.) *Olduvai Gorge, 1959–1961*, Cambridge: Cambridge University Press, pp. 109–123.

Faure, M. (1986). Les Hippopotamidés du Pléistocène ancien d'Oubeidyeh (Israël). In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jordain à Oubeidiyeh*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem **5**, pp. 107–142.

Ficcarelli, G., Torre, D. & Turner, A. (1984). First evidence for a species of raccoon dog, *Nyctereutes* Temminck, 1838, in South-African Plio-Pleistocene deposits. *Bolletino della Societá Paleontologica Italiana* **23**, 125–130.

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher III, C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S., Bosinski, G., Jöris, O., de Lumley, M., Majsuradze, G. & Mouskhelishvili, A (2000). Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. *Science* **288**, 1019–1025.

Geraads, D. (1979). Nouvelles donnés sur *Hyena brevirostris bathygnata* Dubois (Carnivora, Mammalia) du Pléistocène de Java. *Comptes Rendus Somm. Societé. Géologique France* **2**, 80–82.

Geraads, D. (1981). Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algérie). *Bulletin Museum National d'Histoire Naturelle, Paris* **3**, 47–86.

Geraads, D. (1986). Les ruminants du Pléistocène d'Oubeidiyeh (Israël). In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jordain à Oubeidiyeh*, Mémoires et Travaux du Centre de Recherche Français de Jérusalem **5**, pp. 143–181.

Geraads, D. (1993). *Kolpochoerus phacochoeroides* (Thomas, 1884) (Suidae, Mammalia) du Pliocène supérieur de Ahl al Oughlam (Casablanca, Maroc). *Geobios* **26**, 731–743.

Geraads, D. (1997). Carnivores du Pliocène terminal de Ahl al Oughlam (Casablanca, Maroc). *Géobios* **30**, 127–164.

Geraads, D., Guérin, C. & Faure, M. (1986). Les suidés du Pléistocène ancien d'Oubeidiyeh (Israël). In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jordain à Oubeidiyeh*, Mémoires et Travaux du Centre de Recherche Français de Jerusalem **5**, pp. 193–105.

Geraads, D. & Tchernov, E. (1983). Fémurs humains du Pléistocène moyen de Gesher Benot Ya'acov (Israel). *L'Anthropologie* **87**, 138–141.

Gibert, J., Ribot, F., Gibert, L., Leakey, M. G., Arribas, A. & Martínez-Navarro, B. (1995). Presence of the Cercopithecid genus *Theropithecus* in Cueva Victoria (Murcia, Spain). *Journal of Human Evolution* **28**, 487–493.

Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabota, C., Palombo, M. R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E. & Torre, D. (1997). Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy: The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia* **103**, 369–388.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–947.

Goren-Inbar, N., Sharon, G., Melamed, Y. & Kislev, M. (2002). Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov. *Proceedings of the National Academy of Sciences USA* **99**, 2455–2460.

Gupta, V. J. & Sahni, A. (1981). *Theropithecus delsoni*, a new cercopithecine species from the Upper Siwaliks of India. *Bulletin of the Indian Geological Association* **14**, 69–71.

Haas, G. (1970). *Metridichoerus evronensis* n. sp., a new Middle Pleistocene phacochoeroid from Israel. *Israel Journal of Zoology* **19**, 179–181.

Harris, J. M. (1983). Family Suidae. In (J. M. Harris, Ed.) *Koobi Fora Research Project, Vol. 2. The Fossil Ungulates: Proboscidea, Perissodactyla, and Suidae*. Oxford: Clarendon Press, pp. 215–302.

Harris, J. M. (1991). Family Bovidae. In (J. M. Harris, Ed.) *Koobi Fora Research Project, Vol. 3. The Fossil Ungulates: Geology, Fossil Artiodactyls and Paleoenvironments*. Oxford: Clarendon Press, pp. 139–320.

Harris, J. M., Brown, F. H. & Leakey, M. G. (1988). Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science, Natural History Museum of Los Angeles County* **399**, 1–128.

Harris, J. M. & White, T. D. (1979). Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society* **69**, 1–128.

Hemmer, H. (2001). Die Feliden aus dem Epivillafranchium von Untermassfeld. In (R.-D. Kahlke, Ed.) *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), Vol. 3*, pp. 699–782.

Hooijer, D. A. (1958). An Early Pleistocene mammalian fauna from Bethlehem. *Bulletin of the British Museum (Natural History) Geology* **3**, 267.

Hooijer, D. A. 1959. Fossil mammals from Jisr Banat Yaqub, South of Lake Huleh, Israel. *Bulletin Research Council of Israel* **8G**, 177–199.

Hooijer, D. A. 1960. A *Stegodon* from Israel. *Bulletin Research Council of Israel* **9G**, 104–107.

Howell, F. C. & Petter, G. (1976). Carnivora from the Omo Group Formations, Southern Ethiopia. In (Y. Coppens, F. C. Howell, G. L. Isaac & R. C. Leakey, Eds.) *Earliest Man and Environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press, pp. 314–331.

Howell, F. C. & Petter, G. (1980). The *Pachycrocuta* and *Hyaena* lineages (Plio-Pleistocene and extant species of the Hyaenidae); their relationships with Miocene ictitheres: *Palhyaena* and *Hyaenictitherium*. *Geobios* **13**, 579–623.

Kalb, J. E. (1995). Fossil elephantoids, Awash paleolake basins, and the Afar triple junction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **114**, 357–368.

Kahlke, R. D. (Ed.) (1997). Das Pleistozän von Untermassfeld bei Meiningen (Thüringen). *Römisch-Germanisches Zentralmuseum* **1**, 1–418.

Kahlke, R. D. (Ed.) (2001a). Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), *Römisch-Germanisches Zentralmuseum* **2**, 419–698.

Kahlke, R. D. (Ed.) (2002b). Das Pleistozän von Untermassfeld bei Meiningen (Thüringen), *Römisch-Germanisches Zentralmuseum* **3**, 699–1030.

Kostopoulos, D. (1997). The Plio-Pleistocene artiodactyls (Vertebrata, Mammalia) of Macedonia 1. The fossiliferous site "Apollonia-1," Mygdonia Basin of Greece. *Geodiversitas* **19**, 845–875.

Koufos, G. & Kostopoulos, D. (1997). New carnivore material from the Plio-Pleistocene of Macedonia (Greece) with the description of a new canid. *Münchner Geowiss. Abh. (A)* **34**, 33–63.

Kurtén, B. (1962). The sabre-toothed cat *Megantereon* from the Pleistocene of Java. *Zoologische Mededelingen, Uitgegeven door het Rijksmuseum van Natuurlijke Historie, Leiden Deel* XXXVIII **6**, 101–104.

Kurtén, B. & Crusafont, M. (1977). Villafranchian carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain). *Commentationes Biologicae* **85**, 1–39.

Leakey, M. G. (1976). Carnivora of the Lake Rudolf succession. In (Y. Coppens, F. C. Howell, G. L. Isaac & R. C. Leakey, Eds.) *Earliest Man and Environments in the Lake Rudolf Basin*. Chicago: University of Chicago Press, pp. 302–313.

Leakey, M. G. (1993). Evolution of the *Theropithecus* in the Turkana Basin. In (N. G. Jablonski, Ed.) *Theropithecus: The Rise and Fall of a Primate Genus*. Cambridge: Cambridge University Press, pp. 85–123.

Lister, A. & Sher, A. (2001). The origin and evolution of the woolly mammoth. *Science* **294**, 1094–1097.

Lumley, H. de, Lordkipanidze, D., Féraud, G., Garcia, T., Perrenoud, C., Falguères, C., Gagnepain, J., Saos, T. & Voinchet, P. (2002). Datation par la méthode ^{40}Ar/^{39}Ar de la couche de cendres volcaniques (couche VI) de Dmanisi (Géorgie) qui a livré des restes d'hominidés fossiles de 1,81 Ma. *Comptes Rendus Palevol.* **1**, 181–189.

Martínez-Navarro, B. (1991). *Revisión Sistemática y Estudio Cuantitativo de la Fauna de Macromamíferos del Yacimiento de Venta Micena (Orce, Granada)*. Unpublished Ph.D. Thesis, Universidad Autónoma of Barcelona.

Martínez-Navarro, B. (1992a). Revisión sistemática de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada, España). In (J. Gibert, Ed.) *Proyecto Orce-Cueva Victoria (1988–1992): Presencia Humana en el Pleistoceno Inferior de Granada y Murcia, Ayuntamiento de Orce*, pp. 21–85.

Martínez-Navarro, B. (1992b). *Megantereon* sp. (Carnivora, Mammalia) de Venta Micena (Orce, Granada, España). *Revista Española de Paleontología* **Extra**, 113–117.

Martínez-Navarro, B., Belmaker, M., & Bar-Yosef, O. (n.d.). Carnivores and bovids from 'Ubeidiya (in prep.).

Martínez-Navarro, B. & Palmqvist, P. (1995). Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science* **22**, 569–582.

Martínez-Navarro, B. & Palmqvist, P. (1996). Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science* **23**, 869–872.

Martínez-Navarro, B. & Palmqvist, P. (1999). Venta Micena (Orce, Granada, Spain): Human activity in a hyena den during the Lower Pleistocene. In (S. Gaudzinski & E. Turner, Eds.) *Proceedings of the Workshop "The Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages," Monrepos, 1995*. Monographien des Römisch-Germanisches Zentralmuseums **42**, 57–71.

Martínez-Navarro, B., Palmqvist, P., Arribas, A. & Turq, A. (1997). La adaptación a una dieta carnívora: Clave de la primera dispersión humana fuera de África en el Pleistoceno inferior. *Senderos de la Evolución Humana,* *Estudios en Homonaje a Phillip V. Tobias, Ludus Vitalis* **1**, 179–204.

Martínez-Navarro, B., Rabinovich, R. & Goren-Inbar, N. (2000). Preliminary study of the fossil Bovidae assemblage from the late Lower Pleistocene archaeological site of Gesher Benot Ya'aqov (northern Israel). *Abstracts of 2000 Meeting of the INQUA-SEQS "The Plio-Pleistocene Boundary and the Lower/Middle Pleistocene Transition: Type Areas and Sections."* Bari, Italy.

Martínez-Navarro, B. & Rook, L. (n.d.). Gradual evolution in the African hunting dog lineage: Systematic implications. *Comptes Rendus Palevol*. (in press).

Martínez-Navarro, B. & Shabel, A. B. (n.d.). The first human migration out of Africa: New faunal evidence from India (in prep.).

Martínez-Navarro, B., Turq, A., Agustí, J. & Oms, O. (1997). Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution* **33**, 611–620.

Mashchenko, E. N. (1994). *Papio* (*Paradolichopithecus*) *suschkini* (Trofimov) – revision of systematics, morpho-functional features of skull and lower mandible. *Paleotheriologya*, 15–17.

Moyà-Solà, S., Agustí, J., Gibert, J. & Vera, J. A. (Eds.) (1987). Geología y paleontología del Pleistoceno inferior de Venta Micena. *Paleontologia i Evolució, Memoria Especial* **1**, 1–297.

Napoleone, G., Albanielli, A., Azzaroli, A., Bertini, A., Magi, M. & Mazzini, M. (2003). Calibration of the Upper Valdarno Basin to the Plio-Pleistocene for correlating the Apennine continental sequences. *Il Quaternario, Italian Journal of Quaternary Sciences* **16**(**Bis**), 131–166.

Oms, O., Parés, J. M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez-Fernández, G. & Turq, A. (2000). Early human occupation of western Europe: Paleomagnetic dates for two Paleolithic sites in Spain. *Proceedings of the National Academy of Sciences USA* **97**, 10666–10670.

Palmqvist, P. (2002). On the presence of *Megantereon whitei* at the South Turkwell hominid site, northern Kenya. *Journal of Paleontology* **76**, 920–930.

Palmqvist, P. & Arribas, A. (2001). Taphonomic decoding of the paleobiological information locked in a Lower Pleistocene assemblage of large mammals. *Paleobiology* **27**, 512–530.

Palmqvist, P., Martínez-Navarro, B. & Arribas, A. (1996). Prey selection by terrestrial carnivores in a Lower Pleistocene paleocommunity. *Paleobiology* **22**, 514–534.

Pickford, M. (1993). Climatic change, biogeography, and *Theropithecus*. In (N. G. Jablonski, Ed.) *Theropithecus: The Rise and Fall of a Primate Genus.* Cambridge: Cambridge University Press, pp. 227–243.

Pickford, M. (1994). Fossil Suidae of the Albertine Rift, Uganda-Zaire. In (B. Senut & M. Pickford, Eds.) *Geology and Paleobiology of the Albertine Rift Valley, Uganda-Zaire, Paleobiology, Vol. II*. Orléans: Cifeg, pp. 339–373.

Pilgrim, G. E. (1939). The fossil Bovidae of India. *Mem. Geol. Surv. India Palaeont. Indica, Calcutta,* n.s. **26**, 1–356.

Radulesco, C. & Samson, P. (1990). The Plio-Pleistocene mammalian succession of the Oltet Valley, Dacic Basin, Romania. *Quatärpaläontologie* **8**, 225–232.

Radulesco, C. & Samson, P. (2001). Biostratigraphy and evolution of the Early Pliocene to Early Pleistocene mammalian faunas of Romania. *Bolletino della Societá Paleontologica Italiana* **40**, 285–291.

Ramirez-Rozzi, F., Walker, C. & Bromage, T. (1999). Early hominid dental development and climate change. In (T. G. Bromage & F. Schrenk, Eds.) *African Biogeography, Climate Change, and Human Evolution*. Oxford: Oxford University Press, pp. 349–363.

Rook, L. (1994). The Plio-Pleistocene Old World *Canis* (*Xenocyon*) ex. gr. *falconeri. Bollettino della Societá Paleontologica Italiana* **33**, 71–82.

Sahnouni, M. & de Heinzelin, J. (1998). The site of Ain Hanech revisited: New investigations at this Lower Pleistocene site in Northern Algeria. *Journal of Archaeological Science* **25**, 1083–1101.

Sickenberg, O. (1967). Die unterpleistozäne Fauna von Wolaks (Griech.-Mazedonien), I. Eine neue Giraffe (*Macedonitherium martinii* nov. gen. nov. spec.) aus dem unteren Pleistozän von Griecheland. *Ann. Géol. Pays Hellén.* **18**, 34–54.

Szalay, F. S. & Delson, E. (1979). *Evolutionary History of the Primates*. New York: Academic Press.

Tchernov, E. (Ed.) (1986). *The Lower Pleistocene Mammals of 'Ubeidiya (Jordan Valley)*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem **5**. Paris: Association Paléorient.

Tchernov, E. (1992). The Afro-Arabian component in the Levantine mammalian fauna: A short bio-geographical review. *Israel Journal of Zoology* **38**, 155–192.

Tchernov, E., Horwitz, L. K., Ronen, A. & Lister, A. (1994). The faunal remains from Evron Quarry in relation to other Lower Paleolithic hominid sites in the Southern Levant. *Quaternary Research* **42**, 328–339.

Thomas, H., Geraads, D., Janjou, D., Vaslet, D., Memesh, A., Billou, D., Bocherens, H., Dobigny, G., Eisenmann, V., Gayet, M., Lapparent de Broin, F. de, Petter, G. & Halawani, M. (1998). First Pleistocene faunas from the Arabian Peninsula: An Nafud desert, Saudi Arabia. *C. R. Acad. Sc. Paris* **326**, 145–152.

Torre, D., Albanielli, A., Bertini, A., Ficarrelli, G., Massini, F. & Napoleone, G. (1996). Paleomagnetic calibration of Plio-Pleistocene mammal localities in central Italy. *Acta Zoologica Cracovensia* **39**, 559–570.

Turner, A. (1986). Miscellaneous carnivore remains from Plio-Pleistocene deposits in the Sterkfontein Valley (Mammalia, Carnivora). *Annals of the Transvaal Museum* **34**, 203–236.

Turner, A. (1987). *Megantereon cultridens* (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibility of a New World origin. *Journal of Palaeontology* **61**, 1256–1268.

Turner, A. (1999). Assessing earliest human settlement of Eurasia: Late Pliocene dispersions from Africa. *Antiquity* **73**, 563–570.

Turner, A. & Antón, M. (1996). The giant hyena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios* **29**, 455–468.

Van der Geer, A. A. E. & Sondaar, P. Y. (2002). The postcranial elements of *Paradolichopithecus arvernensis* (Primates, Cercopithecidae, Papionini) from Lesvos, Greece. In (M. D. Dermitzakis, Ed.) *Annales Géologiques des Pays Helléniques* **39**, 71–86.

Vekua , A. (1972). *Kvabebskaja fauna akcagylskich pozvonocnych*. Moskow (in Russian).

Vekua, A. (1995). Die Wirbeltierfauna des Villafranchian von Dmanisi und ihre biostratigraphische Bedeutung. *Jarhb. Ger.- Röm. Zentralmuseum Mainz* **42**, 77–180.

Vekua, A., Lordkipanidze, D., Rightmire, P., Agusti, J., Ferring, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de Leon, M., Tappen, M., Tvalchrelidze, M. & Zollikofer, C. (2002). A new skull of early *Homo* from Dmanisi, Georgia. *Science* **297**, 85–89.

Vrba, E. S. (1987). A revision of the Bovini (Bovidae) from a preliminary revised checklist of Bovidae from Makapansgat. *Paleontologia Africana* **26**, 33–46.

Werdelin, L. & Lewis, M. E. (2000). Carnivora from the South Turkwell hominid site, northern Kenya. *Journal of Paleontology* **74**, 1173–1180.

Werdelin, L. & Lewis, M. E. (2002). Species identification in *Megantereon*: A reply to Palmqvist. *Journal of Paleontology* **76**, 931–933.

Werdelin, L. & Solounias, N. (1991). The Hyenidae: Taxonomy, systematics and evolution. *Fossils and Strata* **30**, 1–104.

White, T. D. (1995). African omnivores: Global climatic change and Plio-Pleistocene hominids and suids. In (E. S. Vrba, G. H. Denton, T. C. Partridge & L. H. Burckle, Eds.) *Paleoclimate and Evolution with Emphasis on Human Origins*. New Haven: Yale University Press, pp. 369–384.

Chapter IV

Ecological Interactions of Elephantids in Pleistocene Eurasia: *Palaeoloxodon* and *Mammuthus*

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Abstract

Straight-tusked elephants of the genus *Palaeoloxodon* entered Eurasia from Africa and apparently spread rapidly: the earliest reliable records from Europe, China, and the Middle East are all in the range 800–600 Ka. This interval also corresponds to the replacement of *Mammuthus meridionalis* (ancestral mammoth) by *M. trogontherii* in Europe, and it is suggested that the extinction of *M. meridionalis* may have been triggered by the arrival of *P. antiquus*, competing for its woodland habitat.

Introduction

The Elephantidae originated in Africa (Maglio 1973) and, in some ways like the Hominidae, their history has been a succession of emigrations from that continent across the rest of the world. Three genera of the Family Elephantidae are known from the Pleistocene of Eurasia: *Elephas* (the lineage of the living Asian elephant *E. maximus*), *Palaeoloxodon* (generally known in English as the straight-tusked elephant), and *Mammuthus* (the lineage of the mammoth). *Elephas* remains are known from the Middle East, the Indian subcontinent, and southeast Asia, but they are relatively few in number, generally poorly dated, and in need of study. This review therefore focuses on the genera *Palaeoloxodon* and *Mammuthus*. The evolution, ecology, and extinction of these genera have almost always been considered in isolation, but ecological interaction among their constituent species may have been important in driving these processes. This brief review incorporates material from across Eurasia, including the Levant.

Palaeoloxodon

The genus *Palaeoloxodon* was named by Matsumoto (1924) for the Japanese species *P. naumanni* and has also been extensively used for the European species *P. antiquus*, although others have synonymized it with *Elephas* (e.g., Maglio 1973), or have regarded it as a subgenus of *Elephas* (e.g., Shoshani & Tassy 1996). However, recent cladistic studies (Inuzuka & Takahashi n.d.; Davies 2002) confirm *Palaeoloxodon* as a monophyletic group of similar status to *Mammuthus* and *Elephas*, and its generic validity is accepted here.

It is widely accepted, based on similarities of cranium and dentition, that Eurasian species of *Palaeoloxodon* have their origin in the African *P. recki* lineage, common fossils of the African Plio-Pleistocene that span the range ca. 4.0–0.5 Ma (Maglio 1973; Beden 1979; Todd 2001). While *P. recki* shows very broad evolutionary changes in features such as increased molar plate count and reduced enamel thickness, a simple succession of chronosubspecies (Maglio 1973; Beden 1979) is probably an oversimplification of more complex variation in time and space (Todd 2001). None of the nominal subspecies is dentally identical to the more advanced *P. antiquus* (Davies 2002), but Beden (1979, 1983) noted two features shared by *P. recki atavus* and the European *P. antiquus* that can be regarded as synapomorphic: enlarged parietal bosses, forming a double cranial dome, and the marked overhanging crest that extends transversely across the frontal bone of the upper face.

Eurasian *Palaeoloxodon* has been divided into a number of species, of which those currently recognized, aside from island endemic forms, include *P. antiquus* of Europe and *P. namadicus* of India. Maglio (1973) synonymized these species (with *namadicus* the senior name), and although they are undoubtedly similar, there are differences in the orientation of the zygomatic arch (Azzaroli 1966) and in the width of the upper molars (Davies 2002), and they can be retained as separate species pending further comparison. Dubrovo (1955) tentatively recognized a skull from the Kuday-Dag district, Turkmenistan, as the new species *P. turkmenicus*. However, the specimen appears to fall within the range of *P. antiquus* in both dental (Davies 2002) and cranial (Dubrovo 1994) morphology. In the Far East a recent analysis recognizes two species: *P. naumanni* of Japan and *P. huaihoensis* of China and Taiwan (Chang 2004).

The earliest appearance of the genus *Palaeoloxodon* in Europe is in the early Middle Pleistocene. In Italy, *P. antiquus* occurs at low frequency at Slivia, placed just below the Brunhes/Matuyama inversion at 780 Ka, and abundantly at Isernia la Pineta, placed tentatively in the early Brunhes, ca. 700 Ka (Sardella et al. 1998). In Spain, however, a recorded occurrence of *P. antiquus* at Huescar-1 in southern Spain, in deposits of the Guadix-Baza basin complex dated to ca. 800–600 Ka (Mazo 1989), is referable instead to *Mammuthus trogontherii* (Davies 2002). In northern Europe, *P. antiquus* is absent from the early Middle Pleistocene *Mimomys savini* faunas of Voigtstedt, West Runton, and Süssenborn, ca. 700–600 Ka (although elephantid remains are only moderately abundant there), but present in the *Arvicola terrestris cantiana* faunas such as Mosbach and Mauer, ca. 500 Ka (Koenigswald & Heinrich 1999; Stuart & Lister 2001). Stuart & Lister (2001) show that the earliest likely occurrence in central and northern Europe is in the late *M. savini* assemblage from Pakefield/Kessingland, Suffolk, UK, thought to postdate West Runton by perhaps one climatic cycle and therefore dated to ca. 600 Ka.

In the Levant, sites with *Palaeoloxodon* remains are relatively few, but a very important record is from Gesher Benot Ya'aqov in the Jordan Valley. In 1989 a partial skull of *P. antiquus* was discovered in association with stone and wooden artifacts indicative of an Acheulian living-floor (Goren-Inbar et al. 1994). The site was originally dated, based on geochronological evidence, to ca. 500 Ka. However, recent paleomagnetic studies indicate an age approximately at the Brunhes-Matuyama boundary, ca. 780 Ka (Goren-Inbar et al. 2000).

Various supposedly earlier records of *Palaeoloxodon* in Europe and western Asia do not withstand close scrutiny. A record from Yakari Sögiitönu in Asiatic Turkey, for example, supposedly dated to ca. 2 Ma (Becker-Platen et al. 1975), was based on a single carpal bone (a lunar), but characters for the separation of this bone between *Palaeoloxodon* and *Mammuthus meridionalis*, the dominant elephantid of this time-interval, have not been ascertained.

In India, the earliest occurrences of *P. namadicus* are from the Narbadda Valley, including the type skull of the species. Although the exact age of this site is unknown, Maglio (1973) correlated it faunally with the Cromerian of western Europe, specifically West Runton and Süssenborn. This would indicate an early Middle Pleistocene age, ca. 700–600 Ka.

Finally, in the Far East, the arrival of *Palaeoloxodon* was originally placed in the Late Pliocene to Early Pleistocene, ca. 2 Ma, based on remains from the Nihowan Basin in eastern China (Teilhard & Piveteau 1930) and, more recently, from a skull recovered from terrace deposits of the Nihowan Basin and supposed to be of similar age (Wei 1976). However, the deposits at Nihowan are complex, with many horizons present, and it is unclear from where the *Palaeoloxodon* remains were recovered (R. Tedford, personal communication). More recent excavations recovered *Palaeoloxodon* not from the channel itself but from overlying Late Pleistocene loess (R. Tedford, personal communication). It therefore seems likely that the *Palaeoloxodon* material from the Nihowan locality dates to the Late Pleistocene (Jin, personal communication). A recent review of *Palaeoloxodon* sites in the Far East suggests that the earliest remains in China date to ca. 700 Ka and those in Japan to ca. 400 Ka (Chang 2004; Konishi & Yoshikawa 1999).

Reliable records of *Palaeoloxodon* in Eurasia, therefore, show a remarkable consistency in the timing of first records. As far as available material allows, the earliest entry of the genus into the Levant, Europe, India, and the Far East all occurred in the interval ca. 800–600 Ka. The Levantine occurrence may well turn out to be the oldest, as this was the likely route for the African progenitor populations. If, as discussed above, the ancestor (or sister-group) of Eurasian *Palaeoloxodon* is the African *P. recki atavus*, a ghost range of around a million years is implied, as the known stratigraphic range of that subspecies is ca. 2.2–1.7 Ma (Beden 1979; Todd 2001). At present it is unknown whether that ghost range occurred in Africa, or in Eurasia in an area not yet sampled.

The *Palaeoloxodon* genus does not show, in its continental Eurasian history, the profound modification of cranium and dentition seen in the *Mammuthus* lineage. Dental morphology from the early Middle Pleistocene to the Late Pleistocene is remarkably conservative (Davies 2002). Seen in a broader chronological and geographical context, however, the pattern shown by the two genera is not so different. *Palaeoloxodon* underwent most of its evolutionary change in Africa in the interval 4.0–0.5 Ma; its arrival in Eurasia ca. 800 Ka represents a major dispersal, but there was little further morphological change. Mammoths, according to the model outlined by Lister & Sher (2001) and Lister et al. (2004), had also more or less completed their morphological evolution by 0.5 Ma (when the earliest *primigenius*-like forms were already established in northeast Siberia), having begun it in Africa ca. 4 Ma ago; the "changes" in Europe after this interval were largely due to immigration events.

Mammuthus

The earliest known representatives of the mammoth lineage, *Mammuthus subplanifrons,* are known from deposits in southern and East Africa in the interval 5–4 Ma (Maglio 1973; Kalb & Mebrate 1993). The earliest unquestionable *Mammuthus* outside Africa is material from the European localities of Montopoli (Italy) and the Red Crag (England), dated to ca. 2.6–2.5 Ma (Lister & Sher 2001; Lister et al. 2004). However, fossils dating to the interval 3.5–3.0 Ma from the Dacic Basin, Romania, are probably referable to this genus, although identification with *Elephas* cannot be completely ruled out on the basis of the few available dental remains (Lister & van Essen 2003; Lister et al. 2004). The Romanian material bears the name *Mammuthus rumanus* (Stefanescu), and similar molars, also in the interval 3.5–3.0 Ma, are known from China, suggesting an early spread of mammoths across the Eurasian continent (Lister et al. 2004). The Montopoli and Red Crag fossils have been referred to "*Mammuthus gromovi*" (Alexeeva & Garutt), but the validity of this species is questionable, and material of this age is referable either to *M.* cf. *rumanus* (Lister et al. 2004) or to an early form of *M. meridionalis.*

The "southern elephant" or "ancestral mammoth" *Mammuthus meridionalis* is known from numerous European sites in the interval ca. 2.5–1.0 Ma, as well as in southern Siberia and China. In the interval ca. 1.0–0.6 Ma, a complex transition takes place in Europe, resulting in the demise of *M. meridionalis* and its replacement by the "steppe mammoth" *M. trogontherii*. The morphological transformation involves an increase in the number of enamel lamellae in the molars, thinning of molar enamel, substantial increase in crown height, and a shortening and heightening of the mandible and cranium, although well-preserved remains of the latter are sparse. A complex array of populations in Europe through the interval of transition, together with the earlier appearance of *M. trogontherii* morphology in China and northeast Siberia than in Europe, has led to the suggestion that this form originated in the East and spread westwards by migration and/or gene flow, progressively supplanting the indigenous *M. meridionalis* (Ferretti 1999; Lister & Sher 2001; Lister et al. 2004). The earliest records of mammoths akin to *M. trogontherii* are ca. 2.0–1.4 Ma in China (Wei et al. 2003) and ca. 1.2–0.8 Ma in northeast Siberia (Lister & Sher 2001). The earliest hints of its appearance on the fringes of the European continent are at the Sinyaya Balka locality on the Black Sea, in Tamanian deposits of ca. 1.0 Ma (Sher 1999; Lister & Sher 2001). By 0.8 Ma it had appeared in central and western Europe, alongside the latest *M. meridionalis*.

The pattern of movement of *M. trogontherii* from the Far East to Europe remains to be determined in detail, and mammoth fossils from intervening areas assume especial importance. Mammoth remains from 'Ubeidiya in the Jordan Valley, Israel, described by Beden (1986), are of interest in this respect. Dated to ca. 1.4–1.5 Ma on the basis of an extensive mammalian fauna (Tchernov 1987; Belmaker et al. 2002), the sample of mammoth molars from 'Ubeidiya is contemporary with *M. meridionalis* in Europe. However, the morphology at 'Ubeidiya is clearly advanced over typical European *M. meridionalis* in several respects (Beden 1986) and may indicate coexistence of that taxon with *M. trogontherii* (Lister n.d.). Given their geographical position, the 'Ubeidiya mammoths may therefore provide evidence of very early "leakage" of *trogontherii*-like morphology from the Far East. Later, in the Middle Pleistocene, only *M. trogontherii* is known from the Middle East, as in Europe. The best-known record is that of Latamné, Syria; I agree with Hooijer's (1961) original identification of the Latamné remains as *M. trogontherii*, contrary to Maglio's (1973) reidentification as *Palaeoloxodon*. However, the sampling in this region is unfortunately not yet nearly complete enough to hazard a guess as to the date of demise of *M. meridionalis*.

Ecological and evolutionary interaction between *Palaeoloxodon* and *Mammuthus*

The above accounts indicate that the late Early and early Middle Pleistocene (ca. 1.0–0.5 Ma) were critical times for elephantids in Eurasia. In general, however, the evolutionary and migrational patterns of the different genera have been considered in isolation. Viewing the history of *Palaeoloxodon* and *Mammuthus* together highlights some patterns that may have evolutionary and ecological significance.

Figure 1 summarizes what is known of the first and last appearance data for selected elephantid taxa in different regions of Eurasia. The entry of *Palaeoloxodon*, as discussed above, is rather constant at ca. 0.8–0.6 Ma throughout. However, in *Mammuthus* the timing of events is more varied. In China, the latest dated *M. meridionalis* is as early as 2 Ma, and only mammoths of *M. trogontherii* morphology are recorded with certainty after that date (Wei et al. 2003, and personal communication). This corresponds to the model whereby the Far East was the locus of transformation between these two species; in other words, one portion of the global *M. meridionalis* range was transformed there into *M. trogontherii*, an apparent local anagenesis that in a broader geographical context can be seen as part of a cladogenetic event. In this situation, one would not expect the local co-occurrence, or overlap in time, of the ancestor (*M. meridionalis*) and descendant (*M. trogontherii*). *Palaeoloxodon* did not enter the area until much later, by which time *M. trogontherii* was firmly established.

In Europe, the situation is different. If *M. trogontherii* appeared as an immigrant from the East, then an overlap between it and local European *M. meridionalis* populations is possible, and several localities provide evidence of this pattern (Lister et al. 2004). As indicated above, the earliest indications of *M. trogontherii* morphology are ca. 1.0 Ma, while *M. meridionalis* morphology seems to persist until ca. 0.8–0.7 Ma. The point of interest is that the appearance of *Palaeoloxodon* in Europe is also placed in the interval ca. 0.8–0.7 Ma. This suggests a possible causal link, in particular that the extinction of *M. meridionalis* in Europe might have been influenced by the arrival of *Palaeoloxodon*. *M. meridionalis*, with its low tooth crowns and small enamel plate number, is generally regarded as a woodland browser, a fact consistent with paleovegetational evidence from localities where it occurs (e.g., Tegelen, the Netherlands; Zagwijn 1963).

In its pattern of occurrence throughout Middle and Late Pleistocene Europe, *Palaeoloxodon antiquus* appears

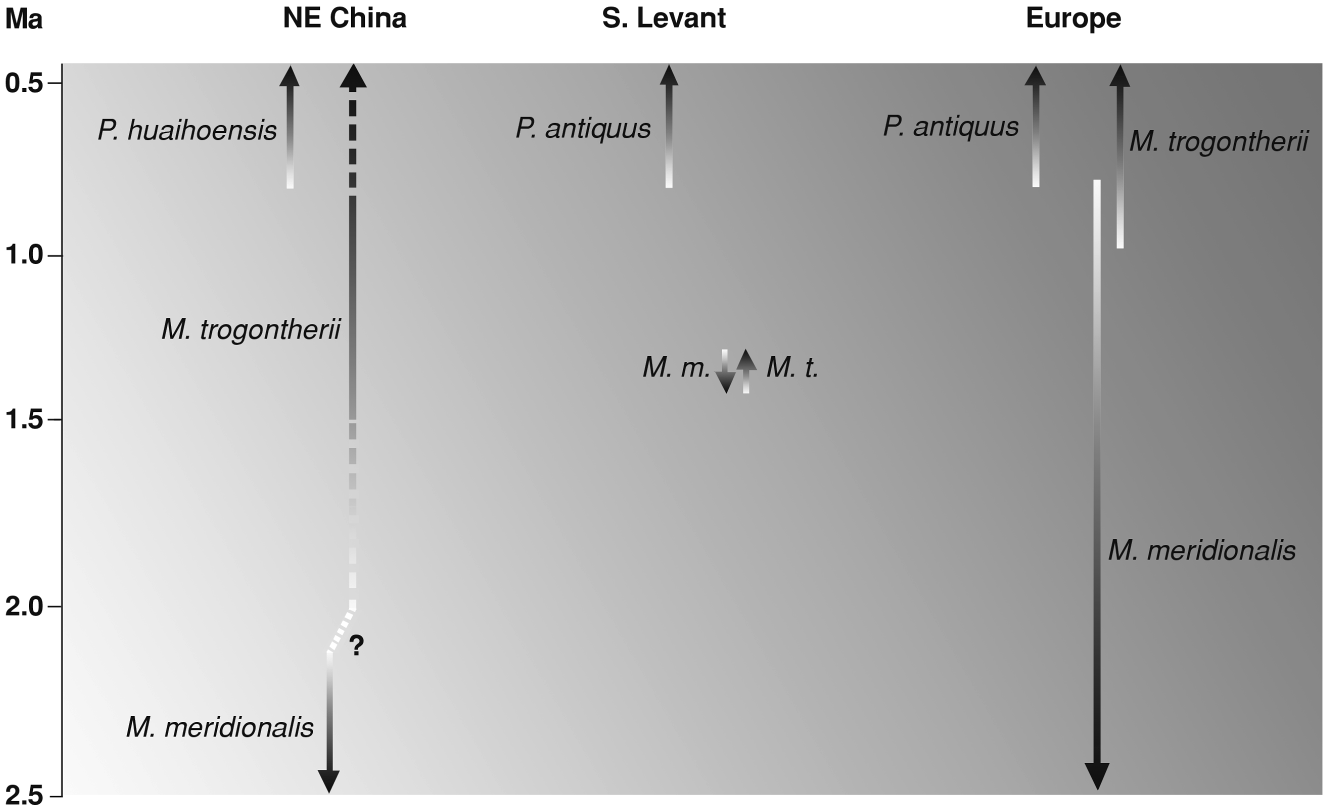

Figure 1. Known time-ranges of selected elephantid taxa in Eurasia: *Mammuthus meridionalis*, *M. trogontherii*, *Palaeoloxodon* spp. Solid lines – known occurrence; dashed lines – likely occurrence; dotted line – suggested evolutionary transition. Records from the southern Levant are based on Gesher Benot Ya'aqov (*P. antiquus*) and 'Ubeidiya (*Mammuthus*; possible co-occurrence of *M. meridionalis* and *M. trogontherii*).

to be strongly linked to temperate, wooded, or mixed vegetational conditions (Stuart 1982), as reflected in its German vernacular name *Waldelefant* ("wood elephant"). Thus, in northern and central Europe, the species occurs in all temperate interglacial phases of the Late Middle and Late Pleistocene (OIS stages 11, 9, 7, 5e), but is generally absent from assemblages assigned to intervening cold stages of generally open habitat (Stuart 1982; Schreve 2001). A record from Greece dated to OIS 6 indicates a Mediterranean refugium (Tsoukala & Lister 1998) in an area where forest survived even through even-numbered OIS stages (Tzedakis 1993).

In part, then, *P. antiquus* can be seen as an ecological replacement for *M. meridionalis*, and the disappearance of the latter at roughly the time of entry of *P. antiquus* suggests a possible competitive effect. The ecological match may not have been perfect: dentally, *P. antiquus* was higher-crowned than *M. meridionalis*, and some records suggest an ability to adapt to semi-open conditions (Lister et al. 1990). We might envisage it as a woodland-adapted animal with a mixed browse and graze diet, in some respects similar to the living Asian elephant (*Elephas maximus*).

The spread of *M. trogontherii* across Europe in roughly the same interval is also of relevance. This species shows very significant advance in these dental parameters over *M. meridionalis*, strongly suggesting a larger grass component of the diet. In its most abundant occurrences in Europe, such as at Mosbach and Süssenborn, it is generally regarded as forming part of a savanna or steppic assemblage of mammals (Koenigswald & Heinrich 1999), although direct paleovegetational evidence is sparse. In other localities (e.g., West Runton, UK), *M. trogontherii* occurs in more mixed environments with woodland as well as open, grassy areas (Stuart 1996).

If *M. trogontherii* evolved elsewhere and entered Europe already ecologically separated from *M. meridionalis*, the two had potential to coexist, albeit in adjacent patches of differing habitat and possibly complicated by hybridization between them (Lister & Sher 2001; Lister et al. 2004). Sites at which such coexistence is suggested, however, all slightly predate the local appearance of *P. antiquus.* At present, there does not appear to be any locality at which *M. meridionalis* and *P. antiquus* can reliably be shown to coexist in a single horizon, either in southern Europe, where *P. antiquus* may have arrived somewhat earlier (Sardella et al. 1998, their Figure 2), or in northern and central Europe, where it arrived a little later (Stuart & Lister 2001). This suggests that any coexistence between them, required for a competition model, was short-lived. Only further dated occurrences of these species can test this question. In any event, what we observe is a *meridionalis-trogontherii* phase (e.g., in northern and central Europe, Dorn-Durkheim, Voigstedt; ca. 800–700 Ka), followed by an *antiquus-trogontherii* phase (e.g., Pakefield, Mosbach, Mauer; ca. 600–500 Ka). The impression is that the ecological patchwork could at most support two elephant species, and that with the arrival of *P. antiquus*, *M. meridionalis* was forced out. The alternative scenario, that *M. meridionalis* died out first, vacating its niche and allowing the colonization of *P. antiquus*, cannot however be ruled out.

Finally, for the Middle East, little can yet be said due to lack of data. If the dating of ʻUbeidiya is correct, mammoths of *M. trogontherii* morphology may have entered the region as early as 1.4 Ma. *P. antiquus* is not recorded until much later, ca. 780 Ka. The date of persistence of *M. meridionalis* is not evidenced, however, so any causal effect of the arrival of *P. antiquus* is unknown at present.

Acknowledgments

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References

Azzaroli, A. (1966). La valeur des caractères crâniens dans la classification des éléphants. *Eclogae Geologicae Helvetiae* **59**, 541–564.

Becker-Platen, J. D., Sickenberg, O. & Tobien, H. (1975). Die Gliederung der känozoischen Sedimente der Türkei nach Vertebraten – Faunen gruppen. *Geologisches Jahrbuch* **B15**, 19–45.

Beden, M. (1979). *Les Eléphants (Loxodonta et Elephas) d'Afrique Orientale: Systématique, Phylogénie, Intérêt Biochronologique. Vols. I & II*. Thèse Doctorat es Sciences, Faculté des Sciences de l'Université de Poitiers.

Beden, M. (1983). Family Elephantidae. In (J. M. Harris, Ed.) *Koobi Fora Research Project. Vol. 2. The Fossil Ungulates: Proboscidea, Perissodactyla and Suidae*. Oxford: Clarendon, pp. 40–129.

Beden, M. (1986). Le mammouth d'Oubeidyeh (Israel). In (E. Tchernov, Ed.) *Les Mammifères du Pléistocène Inférieur de la Vallée du Jourdain à Oubeidiyeh*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem 5. Paris: Association Paléorient, pp. 213–234.

Belmaker, M., Tchernov, E., Condemi, S. & Bar-Yosef, O. (2002). New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *Journal of Human Evolution* **43**, 43–56.

Chang, C.-H. (2004). *Biostratigraphy, Palaeoecology and Evolution of Elephantidae in the Quaternary of the Far East*. Unpublished PhD Thesis, University of London.

Davies, P. (2002). *The Straight-tusked Elephant, Palaeoloxodon antiquus, in Pleistocene Europe*. Unpublished PhD Thesis, University of London.

Dubrovo, I. A. (1955). New data on morphology and distribution of ancient elephants (*Hesperoloxodon*). *Reports, Academy of Science of the USSR* **101**, 759–762 (in Russian).

Dubrovo, I. A. (1994). Fossil elephants from the Common-wealth of Independent States. In (L. D. Agenbroad & J. I. Mead, Eds.) *The Hot Springs Mammoth Site: A Decade of Field and Laboratory Research in Paleontology, Geology, and Paleoecology*. Hot Springs, SD: The Mammoth Site, pp. 426–451.

Ferretti, M. P. (1999). *Mammuthus meridionalis* (Mammalia, Proboscidea, Elephantidae) from the "Sabbie Gialle" of Oriolo (Cava La Salita, Faenza, northern Italy) and other European populations of southern mammoth. *Eclogae Geologicae Helvetiae* **92**, 503–515.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–947.

Goren-Inbar, N., Lister, A. M., Werker, E. & Chech, M. (1994). A butchered elephant skull and associated artifacts from the Acheulian site of Gesher Benot Ya'aqov, Israel. *Paléorient* **20**, 99–112.

Hooijer, D. A. (1961). Middle Pleistocene mammals from Latamné, Orontes Valley, Syria. *Annales Archéologiques de Syrie* **11**, 117–132.

Inuzuka, N. & Takahashi, K. (n.d.). Discrimination between the genera *Palaeoloxodon* and *Elephas* and the independent taxonomical position of *Palaeoloxodon* (Mammalia: Proboscidea). In (S. Rubio, Ed.) *Homenaje a Emiliano Aguirre*. Alcalá de Henares: Museo Arqueológico Regional (in press).

Kalb, J. E. & Mebrate, A. (1993). Fossil elephantoids from the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Transactions of the American Philosophical Society* **83**, 1–114.

Konishi, H. & Yoshikawa, S. (1999). Immigration times of the two proboscidean species, *Stegodon orientalis* and *Palaeoloxodon naumanni*, into the Japanese Island and the formation of the land bridge. *Earth Science* **53**, 125–134 (in Japanese with English abstract).

Lister, A. M. (n.d.). Evolutionary and biostratigraphic implications of elephantid remains from 'Ubeidiya, Jordan Valley, Israel. In (L. K. Horwitz, R. Rabinovich & O. Bar-Yosef, Eds.) *The Diversity of Archaeofaunas in the Southern Levant*. American School of Prehistoric Research Monographs. Cambridge and Boston: Harvard University, Peabody Museum and Brill Academic Publishers (in prep.).

Lister, A. M., Keen, D. H. & Crossling, J. (1990). Elephant and molluscan remains from the base of the Baginton-Lillington Gravels at Snitterfield, Warwickshire. *Proceedings of the Geologists' Association* **101**, 203–212.

Lister, A. M. & Sher, A. V. (2001). The origin and evolution of the woolly mammoth. *Science* **294**, 1094–1097.

Lister, A. M., Sher, A. V., Van Essen, H. & Wei, G. (2004). The pattern and process of mammoth evolution in Eurasia. *Quaternary International* (in press).

Lister, A. M. & Van Essen, H. (2003). *Mammuthus rumanus* (Stefanescu), the earliest mammoth in Europe. In (A. Petulescu & E. Stiuca, Eds.) *Advances in Vertebrate Paleontology "Hen to Panta"*. Bucharest: Romanian Academy Institute of Speleology "Emil Racovita", pp. 47–52.

Maglio, V. J. (1973). Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* **63**, 1–149.

Matsumoto, H. (1924). Preliminary note on fossil elephants in Japan. *Journal of the Geological Society of Tokyo* **31**, 255–272.

Mazo, A. V. (1989). Nuevos restos de Proboscidea (Mammalia) en la Cuenca de Guadix-Baza. *Trabajos Sobre el Neogeno-Cuaternario* **11**: *Geologia y Paleontologia de la Cuenca de Guadix-Baza*, 225–237.

Sardella, R. et al. (1998). Mammal faunal turnover in Italy from the Middle Pliocene to the Holocene. *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO* **60**, 499–511.

Schreve, D. C. (2001). Differentiation of the British late Middle Pleistocene interglacials: the evidence from mammalian biostratigraphy. *Quaternary Science Reviews* **20**, 1693–1705.

Sher, A. V. (1999). The identity of the Tamanian elephant. In (J. W. F. Reumer & J. de Vos, Eds.) *Second International Mammoth Conference, Abstracts*. Rotterdam: Natuur Museum, pp. 56–58.

Shoshani, J. & Tassy, P. (1996). *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*. Oxford: Oxford University Press.

Stuart, A. J. (1982). *Pleistocene Vertebrates in the British Isles*. London: Longman.

Stuart, A. J. (1996). Vertebrate faunas from the early Middle Pleistocene of East Anglia. In (C. Turner, Ed.) *The Early Middle Pleistocene of Europe*. Rotterdam: Balkema, pp. 9–24.

Stuart, A. J. & Lister, A. M. (2001). The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: Evidence for a new temperate episode in the British early Middle Pleistocene. *Quaternary Science Reviews* **20**, 1677–1692.

Tchernov, E. (1987). The age of the 'Ubeidiya Formation, an Early Pleistocene hominid site in the Jordan Valley. *Israel Journal of Earth Science* **36**, 3–30.

Teilhard de Chardin, P. & Piveteau, J. (1930). Les mammifères fossiles de Nihowan (Chine). *Annales de Paléontologie (Paris)* **19**, 1–154.

Todd, N. E. (2001). African *Elephas recki*: Time, space and taxonomy. In (G. Cavarretta, P. Gioia, M. Mussi & M. R. Palombo, Eds.) *The World of Elephants*. Rome: Consiglio Nazionale delle Ricerche, pp. 693–697.

Tsoukala, E. & Lister, A. M. (1998). Remains of straight-tusked elephant, *Elephas (Palaeoloxodon) antiquus* Falc. & Caut. (1847), ESR-dated to oxygen isotope stage 6, from Grevena (W. Macedonia, Greece). *Bollettino della Societa Paleontologica Italica* **37**, 117–139.

Tzedakis, P. C. (1993). Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* **364**, 437.

Wei , Q. (1976). Recent find of fossil *Palaeoloxodon namadicus* from Nihewan Beds, NW Hebei. *Vertebrata PalAsiatica* **14**, 53–58.

Wei, G., Taruno, H., Jin, C. & Xie, F. (2003). The earliest specimens of the steppe mammoth, *Mammuthus trogontherii*, from the Early Pleistocene Nihewan Formation, North China. *Earth Science (Japan)* **57**, 269–278.

Zagwijn, W. H. (1963). Pollen-analytic investigations in the Tiglian of the Netherlands. *Mededelingen Geologische Stichting (n.s.)* **16**, 49–71.

Chapter V

Long-term Continuity of a Freshwater Turtle (*Mauremys caspica rivulata*) Population in the Northern Jordan Valley and its Paleoenvironmental Implications

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Abstract

Gesher Benot Ya'aqov (ca. 780 Ka) in the Jordan Valley, Israel, is a key site for understanding human dispersals out of Africa through the Levantine Corridor. Turtle shell fragments from this site occur in horizons containing a wealth of anthropogenic and biotic remains. These shell fragments represent *Mauremys caspica*, the only freshwater turtle species presently known from the region. Both fossil and present-day Jordan Valley populations of *Mauremys caspica* share a distinct bony plate shell anomaly, unknown from northern populations of this species. This shared occurrence indicates the genetic continuity of the fossil and recent populations. Data presented herein support this hypothesis. In addition, the continuous existence of this turtle population throughout the Pleistocene argues for environmental stability. Paleoenvironmental reconstruction of the Gesher Benot Ya'aqov site portrays a complex freshwater lake and marshland ecosystem. This rich environment remained little changed until modern times and likely facilitated human dispersals out of Africa.

Introduction

Turtle shell fragments (N=285) from the Middle Pleistocene Paleolithic site of Gesher Benot Ya'aqov (GBY) in the Jordan Valley, Israel, shed light on the paleoenvironment of the region. GBY is dated to ca. 780 Ka (Verosub et al. 1998) and is considered a key site for understanding the dispersal of humans out of Africa (Goren-Inbar et al. 2000, 2002a). All turtle fragments from the GBY horizons are assigned to *Mauremys caspica*, an extant, local freshwater species. This occurrence is the earliest fossil report of this species (Hartman 2001). It is demonstrated herein that the fossil population from the site of GBY and the present population of *M. caspica* from the Jordan Valley represent a genetic continuum. While a shell anomaly in the carapace is shared by both the recent and fossil populations from the Jordan Valley, this anomaly is absent in northern populations of the species (Cherepanov 1994). Furthermore, data demonstrate that the presence of anomalies in turtle shells can be used to distinguish between discrete populations of a single species inhabiting different localities. This feature has useful paleoenvironmental implications.

New excavations at the Lower Paleolithic site of GBY were directed by Naama Goren-Inbar of the Hebrew University of Jerusalem between 1989 and 1997. These excavations yielded a wealth of anthropogenic and organic finds. The lithic assemblage from the site contained numerous basalt tools, including handaxes and cleavers, manufactured from double ventral faced flakes (the "Kombewa" technique). This site is the only place outside of Africa where the Kombewa technique and the use of basalt as a raw material have been reported (Goren-Inbar & Saragusti 1996; Sharon 2000). The remarkable preservation of botanical (Melamed 1997; Goren-Inbar et al. 2002b) and faunal remains (Goren-Inbar et al. 1992, 1994, 2000) permits detailed reconstruction of the paleoenvironments that hosted hominids as they dispersed out of Africa through the Levantine Corridor and into Eurasia.

Shell morphology

The turtle shell is a novel structure among vertebrates. The shell consists of two major components: an external layer made of keratinous scutes and an underlying layer comprised of osseous plates (Zangerl 1969; see Figure 1). The osseous component of the shell integrates bones of skeletal (endochondral) and dermal (intramembranous) origin. The plastron or ventral part of the shell is commonly formed from nine intramembranous plates. Other than the single central entoplastron, the plastron plates (epiplastron, hyoplastron, hypoplastron, and xiphiplastron) are paired. These plates are connected medially by sutures and are arranged symmetrically along the longitudinal axis of the plastron.

The dorsal dome-shaped portion of the shell, or carapace, is formed by the fusion of the vertebrae and ribs with intramembranous plates (see Figure 1; Hoffstetter & Gasc 1969; Zangerl 1969; Gilbert et al. 2001). The neural plates, commonly eight in number, comprise the trunk vertebrae and intramembranous plates and lie along the medial axis of the carapace. Additional intramembranous plates comprise the superior and inferior ends of the medial axis and include the nuchal bone, positioned anterior to the neurals, and the suprapygal and pygal bones, positioned posterior to the neurals. Eight pairs of costal plates made of intramembranous bones fuse with the ribs and contact the lateral edge of the neurals. The costal segments form the most substantial part of the carapace structure. The lateral edge of the costal plates is bordered by the peripheral plates. These plates are entirely intramembranous in nature (usually 11 pairs) and extend from the nuchal to the pygal plate, forming the margins of the carapace. All bony plates of the carapace and plastron are overlaid by a thin layer of keratinous scutes.

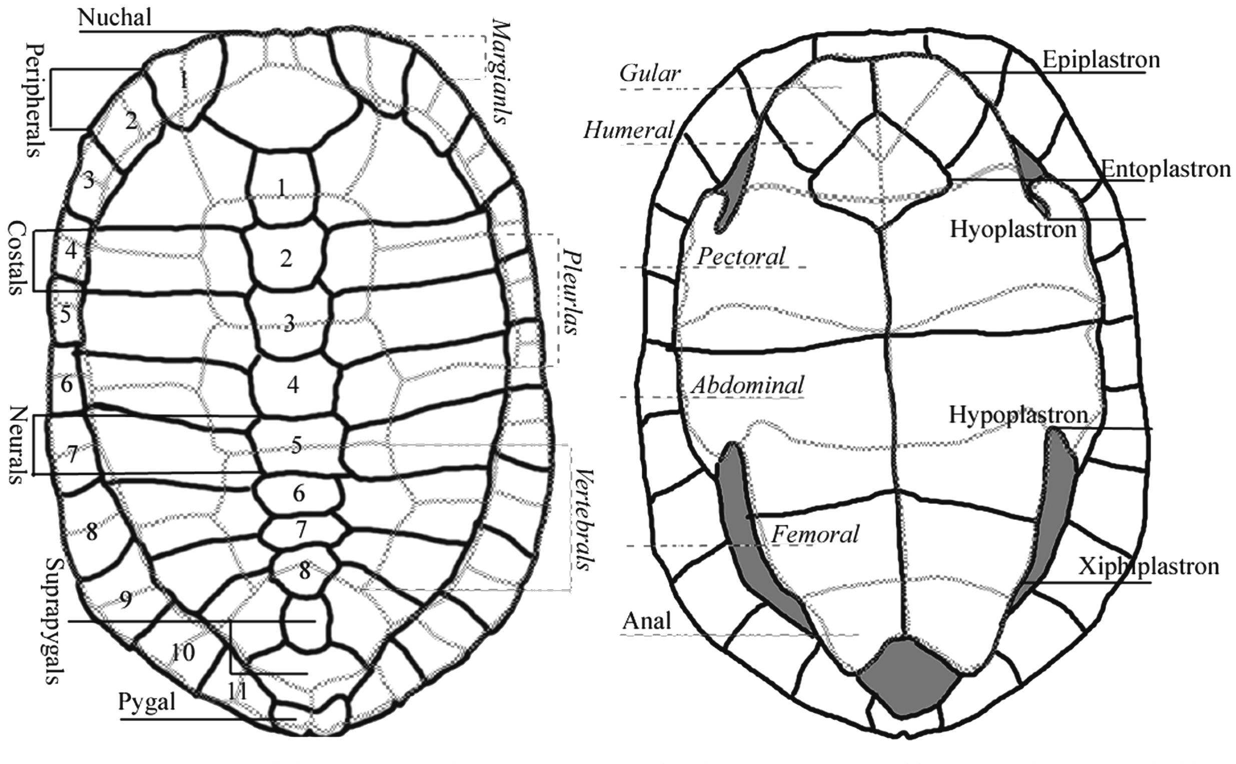

Figure 1. *Mauremys caspica* shell diagram. Left side: carapace; right side: plastron. The external keratinous layer is marked by reticulated lines and its scutes are labelled in *italics*. The internal osseous layer is marked by solid lines. Solid lines also mark the labelled bony plates.

Shortly after the initiation of post-mortem decay, a turtle shell disintegrates into separate bony plates (Bourn & Coe 1979; Dodd 1995). The preservation of non-ossified tissues like keratin is unusual, and thus is only suggested by the impressions of the margins of keratinous scutes on the outer surface of the bony plates.

Significance of variation in shell morphology

Although the evolution of turtle shell morphology has been relatively conservative (Gaffney & Meylan 1988), intraspecific variation in both the number and shape of the keratinous scutes and osseous plates has long been recognized (Gadow 1899; Parker 1901; Newman 1906; Coker 1910; Lynn 1937; Lynn & Ullrich 1950; Zangerl & Johnson 1957). This variation is expressed as the presence of additional bony plates or keratinous scutes. The appearance of additional scutes and plates was initially interpreted as an ancestral (plesiomorphic) condition that has occasionally gained phenotypic expression (e.g., atavism) (Gadow 1899; Newman 1906; see also Gaffney 1990 for a description of the earliest turtle fossil *Proganochelys*). Others described shell anomalies as resulting from environmental factors, such as brush fires or dehydration of eggs during different stages of incubation. Eggs that experience dehydration during critical embryological stages are liable to suffer from severe deformations (Lynn 1937; Lynn & Ullrich 1950; Kazmaier & Robel 2001). It has also been argued that there is an increase in the occurrence of abnormal variation in the keratinous layer throughout a turtle's life. For example, Zangerl & Johnson (1957) found that keratinous anomalies correlate positively with size and age. While this argument corroborates the environmental interpretation, Zangerl & Johnson (1957) acknowledged that some of the reported variation was species- and population-specific, and thus that variation might have a genetic origin (Zangerl & Johnson 1957:361).

Although atavism is no longer an accepted explanation for shell variation, other genetic interpretations have been advanced (Zangerl 1969; Rhodin et al. 1993; Cherepanov 1994). According to Cherepanov (1989, 1997b), who studied the embryonic stages of shell formation in turtles, variation in the number of carapace bone elements is related to the relationship between skeletal (vertebrae and ribs) and dermal elements during development. For example, those segments associated with elements such as vertebrae (neurals) and ribs (costals) tend to be more constrained in their development than those that are not. Most variation in the dermal plates occurs during early stages of ontogeny in plates that form independently of the axial skeleton (nuchal, suprapygal, and pygal). Nevertheless, some anomalous variation in axial segments does occur (Cherepanov 1994, 1997a). Variation can also be caused by anomalies in the formation of keratinous scutes (Cherepanov 1989, 1994). The formation of the external keratinous shield precedes the development of bony plates during the embryonic stage. Because the development of bony plates is externally constrained by the shape of the keratinous scutes, any numerical or morphological deviation in their formulae consequently affects the bony plates.

Regardless of the causes of shell anomalies, the presence of minor variations in the morphology and numerical formulae of the shell apparently is neither advantageous nor detrimental to a turtle's survival. These variations do not alter the hydrodynamic properties of the shell, nor do they have any observed functional role. Natural selection is more likely to act on the shell as a single unit than on individual bony plates. Thus, because they are integrated into the rigid frame of the shell, anomalies should not be selected for or against. The lack of any apparent adverse effect of shell variation on turtle fitness might explain the abundance of shell anomalies across species and localities.

Assuming that selection acts only against bony plate anomalies that cause shell deformations, and if those anomalies that are selectively neutral have a genetic basis (Ann Burke, personal communication, 2003), at least some phenotypic anomalies can be transferred across generations. Therefore, when dealing with long-term populations, one might expect to find persistence in the same bone anomaly over long periods of time. These features, therefore, may serve as evidence for population continuity.

Two conditions must be fulfilled to confirm the population continuity hypothesis: 1) different populations of the same species should be distinguished by differences in the pattern of bony plate anomalies; and 2) typical bony plate anomalies ought to be shared by both fossil and recent populations of the species inhabiting the same geographic location. The status of these two conditions in the Jordan Valley populations of *M. caspica* is examined below.

Mauremys caspica at Gesher Benot Ya'aqov

No testudine cranial remains have been recovered from Pleistocene deposits in Israel, and GBY is no exception; nonetheless, the shell fragments contain sufficient morphological evidence for affiliation with the species *Mauremys caspica*. The earliest Plio-Pleistocene testudine remains from Israel's Jordan Valley were found in the Early Pleistocene (ca. 1.4 Ma) site of 'Ubeidiya (Haas 1966; Bar-Yosef & Goren-Inbar 1993). In his manuscript on the fauna of 'Ubeidiya, Haas (1966) mentions the possible existence of four turtle genera: *Testudo*, *Trionyx*, *Mauremys* (formerly named *Clemmys*), and *Emys*. In addition, a single questionable bone element was assigned to a second sub-order, Pleurodira (side-neck turtles). A comparison of the testudine skeletal plates from GBY and the genera represented at 'Ubeidiya indicates that the GBY plates share characteristics only with the genus *Mauremys* (Hartman 2001; see below).

The pelvis of Pleurodiran turtles is fused to the xiphiplastron plate of the plastron, forming a scar on the ventral surface of the plate. None of the xiphiplastron plates from the site of GBY showed evidence of ventral scarring.

The keratinous layer of the terrestrial tortoise (*Testudo*) shell is thicker than that seen in freshwater turtles. Consequently, the external keratinous layer leaves deep concentric imprints of its growth layers on the outer surface of the bony plates. In freshwater turtles the thin keratinous layer leaves only the sulci created by the edges of the scutes (Pritchard 1979). All of the bony plates from GBY have smooth external surfaces, indicative of the thin keratinous layers typical of freshwater turtles.

The *Trionyx* turtles have highly modified shells, characterized by a reduced bony structure and the absence of the keratinous layer (Ernst & Barbour 1989). The bony plates in this genus are distinguished by rough outer surfaces ornamented with numerous rounded bony outgrowths. No such plates have been recovered from GBY.

The freshwater turtle species *Emys orbicularis* has a few distinctive morphological characters typical of the species: the absence of buttresses in the hyoplastra and hypoplastra that connect the plastron and the carapace; a hinge between the hyoplastra and hypoplastra; and a shallow posterior plastral notch (Ernst & Barbour 1989). The hyoplastra and hypoplastra remains from GBY have well-developed buttresses and deep posterior notches in the xiphiplastra, and lack hinge marks. The turtle remains from GBY thus provide no evidence for the existence of the genus *Emys* in the region during the Middle Pleistocene. This result is important because it counters Fritz's claim (1989; Fritz et al. 1998) that, until the beginning of the twentieth century, the distribution of this genus extended southward from its present-day location in southeastern Turkey to the Jordan Valley.

Mauremys caspica is the only extant freshwater turtle species in the Jordan Valley. The earliest record of *Mauremys* in this region is from the site of 'Ubeidiya. Haas (1966) described the abundant shell remains of this species at 'Ubeidiya as *Mauremys* sp., but not the present-day species *M. caspica* because of considerable dissimilarity in body size. Haas estimated that the fossil turtles were at least one-third larger than modern *M. caspica* from the Jordan Valley. Unlike the fossils from 'Ubeidiya, the turtles from GBY are similar in size to those currently extant in the Jordan Valley (Hartman 2001). Also, the shell morphology and epidermal scute pattern on the bony plates of the fossil turtles are identical to those of modern *M. caspica*. Some of the more diagnostic characters (see Figure 2) include: 1) the external margins of the peripheral bones flare upward, and the flaring is much steeper on the anterior than on the posterior peripherals; 2) a deep transverse furrow, which opens medially into a superiorly projected semicircular depression, transects the ventral face of the nuchal plate; and 3) the external surface of the diamond-shaped entoplastron is transected by sulci from both gular and humeral scutes.

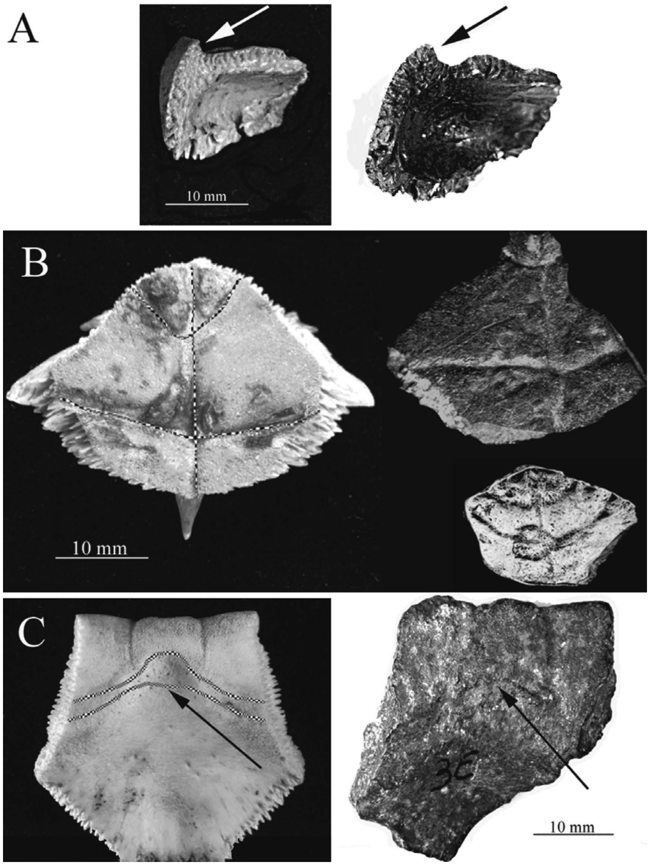

Figure 2. Comparison between recent (left) and fossil (right) bony plate shell elements of *Mauremys caspica* turtles from the upper Jordan Valley of Israel: A) Sagittal view of peripheral number 3. The arrows point to the upward flaring of the plate margins. B) Dorsal view of the diamond-shaped entoplastron. The impressions made by the gular and humeral keratinous scutes are marked by reticulated lines in the recent specimen. C) Ventral view of the nuchal plate. The deep furrow that crosses the plates transversally is marked by reticulated lines in the recent specimen. The superiorly projected semicircular depressions are marked by arrows.

Genetic continuity of the Jordan Valley *Mauremys caspica*

A recent sample of *M. caspica* shells (N=63) was collected from the Hula Nature Reserve in the upper Jordan Valley of Israel, in close proximity (10 km) to the site of GBY. These turtles were the prey of white-tailed eagles (*Haliaeetus albicilla*) nesting in the reserve and represent the natural population of the species in the Jordan Valley today. Based on this sample, a standard carapace formula was determined for the local *M. caspica* population. The formula consists of a single nuchal, 8 neurals, 2 suprapygals, 1 pygal, 8 pairs of costals, and 11 pairs of peripherals (Hartman 2001). It is evident that anomalies in the carapace formula are common among the Hula turtles. Some of these anomalies are repeated in different individuals of the same population (Figure 3). If spontaneous neutral mutations are responsible for the

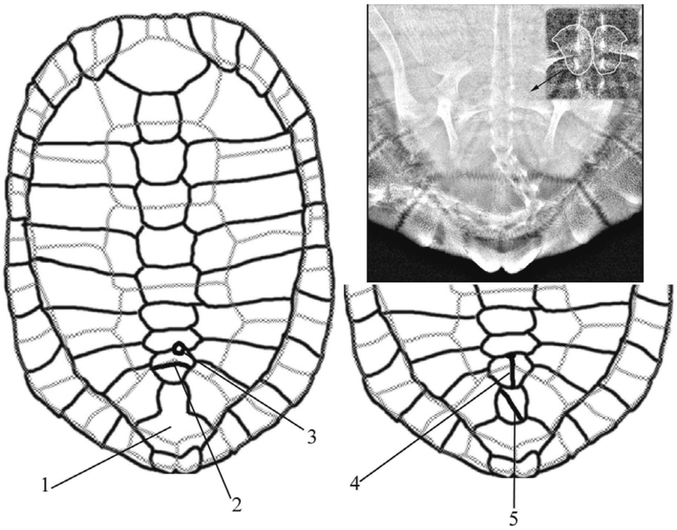

Figure 3. Common bony plate anomalies in *Mauremys caspica* shells from the present-day population of the upper Jordan Valley: 1) suprapygal 1+2 are fused into one plate; 2) neural 8 splits transversally into two plates; 3) additional plate between neural 7 and neural 8; 4) neural 8 splits longitudinally into two plates; 5) suprapygal 1 splits diagonally into two asymmetrical plates. In the upper right corner is an x-ray image of the posterior portion of a shell showing an anomalous longitudinal split of neural 8.

appearance of random bone anomalies, repeated patterns of anomalies likely represent a hereditable trait indicating genetic relatedness. The recovery of fossil *M. caspica* remains from the site of GBY creates a unique opportunity to detect the existence of shell anomalies in the fossil population. Similarity in the pattern and frequency of shell anomalies in fossil and recent populations in the same geographic unit supports an interpretation of genetic continuity.

However, it must first be established that unrelated populations of the same species can be distinguished by the presence/absence or the relative frequencies of their shell anomalies. Unfortunately, the available comparative samples of *M. caspica* are too small to test for statistically significant differences in shell bone plate patterns among populations of this species. To overcome sample size limitations, *Trachemys scripta*, an unrelated but ecologically similar New World species, provides a test case to detect interpopulation variability in shell anomalies within a single species. *T. scripta* was selected because of its abundance in the Smithsonian Institution National Museum of Natural History (USNM) collections in Washington, DC, where the second stage of this research was undertaken. *T. scripta* is also comparable to *Mauremys caspica* in terms of ecology and habitat (Ernst et al. 1994). Both species favor quiet water habitats with soft bottoms (Sidis 1983; Ernst et al. 1994) and have similar dietary preferences (Sidis 1983; Parmenter & Avery 1990). Furthermore, the two species appear in the paleontological record at approximately the same time during the Pleistocene (Seidel & Jackson 1990; Holman 1998). The results of the *T. scripta* test are further discussed in this paper.

Materials and methods

Four populations of the species *Trachemys scripta* (N=104) were randomly selected to test for intraspecific variation in shell anomalies amongst populations of the same species. These turtles were obtained from the USNM dry collections. Three of the populations belong to the subspecies *T. s. elegans* (Rayville, Richland County, Louisiana, N=20; Red River, Concordia County, Louisiana, N=32; Wheeler Reservoir, Tennessee River, Alabama, N=28), and the fourth to the subspecies *T. s. scripta* (Jackson, Marianna County, Florida, N=23).

The fossil turtle bones from the site of GBY consist of 285 fragments of shell and appendicular elements initially identified by Rivka Rabinovich of the Hebrew University of Jerusalem. Differentiation of shell elements was undertaken by examining the morphology and imprint patterns (sulci) left by the keratinous scutes on each element. Anomalies characterized by fused and split plates preserve the original morphology of the bony plate and thus were identifiable to element and species. However, anomalies characterized by deformed plate morphologies or sulci imprints do not preserve features that are diagnostic to *M. caspica* and thus could not be identified to species. Consequently, the only anomalies recorded were of fused or split plates.

Additional turtle shells from populations of the genus *Mauremys* outside of the Jordan Valley were studied to examine possible variation in shell anomalies in comparative turtle populations. These comparative specimens were mostly preserved in ethanol and were obtained from the USNM wet collections. They include *M. caspica* (N=13) and *M. leprosa* (N=27). The *M. caspica* shells originate from diverse geographic areas ranging from Central Asia to the Arabian Peninsula. The sample of *M. leprosa*, a sister taxon of *M. caspica,* originates from North Africa and Spain. Since sample sizes for the different localities were too small for interpopulation comparisons, these shells were primarily used to explore variation in shell morphology within the genus *Mauremys*.

All of the specimens from the USNM collections were radiographed using a Kevex-Varian digital x-ray system. Each turtle was x-rayed at 60 kW and 0.99 mA. The use of nondestructive high resolution radiographs combined with image processing software (Adobe® Photoshop 7®) enabled examination of the bony plates without having to remove the keratinous cover of scutes. The radiograph technique was adequate for the detection of the sutures between shell elements in juvenile and young adult specimens. Old individuals had to be excluded from the analysis due to shell hypermineralization, which obscured the sutures between bone elements and made it impossible to differentiate between individual carapace plates.

Intraspecific variation in shell formulae in Trachemys scripta populations

Of 104 radiographed *Trachemys scripta* specimens, 9 had to be excluded from analysis due to poor image quality. Nearly 20% (19 of 96 individuals) of the remaining radiographed specimens displayed at least one shell anomaly. The distribution of shell anomalies among the four radiographed populations was highly variable (Table 1). Two populations (Rayville, Louisiana [N=17] and Wheeler Reservoir, Alabama [N=27]) had high frequencies (30%) of shell anomalies, whereas the other two (Red River, Louisiana [N=30] and Jackson, Florida [N=22]) had substantially lower frequencies of anomalous individuals (less than 15%).

It is possible to separate at least two of the populations based on the presence/absence of shell anomalies. The population from Rayville, Louisiana, can be distinguished from the other *T. scripta* populations by a rare anomalous division of neural 8 into 3 separate plates (11.8% of sample) and by the equally common occurrence (11.8%) of an additional plate between the nuchal and costal 1. This anomaly is unique to the Rayville population. The population from the Wheeler Reservoir, Alabama, is distinguished by the presence of an additional neural plate (9 instead of 8; 11.1% of sample) and an additional pair of peripheral plates (12 instead of 11; 14.8% of sample). These two anomalies often occur as a suite in association with an additional pair of costals (9 instead of 8), and thus the three anomalies may be developmentally linked. Both the Rayville and Wheeler Reservoir populations are differentiated from the other populations by specific patterns of anomalies. Most anomalies shared between individuals within a population are at the posterior end of the carapace (the last neural and the suprapygals).

Table 1. Description of osseous shell anomalies and frequencies at which they appear in different populations of *Trachemys scripta* in North America.

Type of Anomaly[6]	**Definition of Bony Plate Anomaly**	**Frequency**			
		A[1]	B[2]	C[3]	D[4]
		N=17	N=27	N=22	N=30
Deviation in axial skeleton	7 neurals	1[5]	1	1	1
	9 neurals	0	3	0	0
	Neural 8 splits into 3 plates	2	0	0	0
	9 pairs of costals	0	5	0	2
	Additional plate between neural 7–8 & costal 7–8	1	0	0	0
Anomalous development of keratinous scutes	12 pairs of peripherals	0	4	0	0
	Additional plates between nuchal & costal	2	0	0	0
Irregular bone formation inside dermis	1 suprapygal	1	0	0	2
	3 suprapygals	0	2	1	1
	Neural 8 fused to suprapygal 1	0	1	0	0
Sum[7]		6	8	1	4
Percentage		35.3	29.6	4.5	13.3

[1] (A) Rayville, Richland, Louisiana.

[2] (B) Wheeler Reservoir, Tennessee River, Alabama.

[3] (C) Jackson, Marianna, Florida.

[4] (D) Red River, Concordia, Louisiana.

[5] Numbers refer to absolute frequency of a given anomaly in a locality.

[6] Shell anomaly categories are taken from Cherepanov (1994, 1997b).

[7] Sum of anomalies refers to number of individual shells that show at least one anomaly.

The Wheeler Reservoir and Red River samples share one anomaly, the addition of a posterior pair of costal plates (9 instead of 8; 18.5% of Wheeler Reservoir sample, 6.7% of Red River sample). These two populations cannot be statistically distinguished on the basis of this anomaly's frequency (2 x 2 frequency test for independence $\chi^2 = 1.440$, $p = 0.229$, Fisher's exact test, one-tailed, $p = 0.213$) (Sokal & Rohlf 1981). The significance values for the χ^2 test depend on sample size, and larger samples are required to reach higher levels of significance. Because sample sizes of fossil populations are typically small, differences in the frequency of anomalies are usually inadequate to discriminate between populations of the same species.

Shell variations in recent populations of Mauremys

Of the 63 *Mauremys caspica* specimens examined from the Hula Nature Reserve in the Jordan Valley, approximately 50% showed at least one deviation from the standard bony plate formula of 8 neurals, 8 pairs of costals, 11 pairs of peripherals, 1 nuchal, 2 suprapygal, and one pygal bone (Table 2). All anomalies in plate formulae were limited to the carapace. The normal bony plate formula is based on the dominant shell pattern recorded in the sample. This carapace formula differs from that reported by Cherepanov (1994) for a population of *M. caspica* from the Soviet Union (N=55), in which the majority (71%) of carapaces had only 7 neurals.

The most common shell anomaly in the present-day population of *Mauremys caspica* in the Jordan Valley is the longitudinal split of neural 8 into two plates. This anomaly appeared in nearly 10% of the examined shells. Interestingly, this anomaly has not been reported in a review on bony plate anomalies in the northern population of *M. caspica* as examined by Cherepanov (1994). Based on the presence/absence of this anomaly, the Jordan Valley (*M. c. rivulata*) population, is significantly different from the northern population of the species (*M. c. caspica*) (frequency test: $\chi^2 = 5.03$, $p = 0.003$; see Cherepanov 1994 for data on *M. c. caspica*). The Hula Valley population can thus be distinguished based on the presence and frequency of the longitudinal split of neural 8 (Figure 3).

The radiographed *Mauremys caspica* (N=13) and *Mauremys leprosa* (N=27) specimens from the USNM could not be clustered by locality because these samples were comprised of specimens individually collected from different localities. Two isolated cases of anomalies were

Table 2. Definition and frequency of osseous shell anomalies in the present-day population of *Mauremys caspica* in the Jordan Valley.

Type of Anomaly[1]	**Definition of Bony Plate Anomaly**	**Frequency**[2]
Deviation in axial skeleton	Additional plate between neural 7 & 8	(4) 6%
	Additional plate between neural 2 & costal 1–3	**(1) 2%**
	Neural 8 splits longitudinally into 2 plates	(6) 10%
	Neural 8 splits transversally into 2 plates	(4) 6%
	Neural 8 splits into 5 plates	(2) 3%
	Neural 8 splits into 3 plates	(1) 2%
	Neural 7 splits longitudinally into 2 plates	(2) 3%
Anomalous development of keratinous scutes	Peripheral 5 splits into 2 plates	(1) 2%
	Peripheral 4–6 are fused	(3) 5%
	Additional plate between nuchal & costal 1	(2) 3%
Irregular bone formation inside dermis	Additional plate between peripheral 11 & pygal	(2) 3%
	Additional plate between neural 7 & suprapygal	(1) 2%
	Suprapygal & neural 8 are fused	(2) 3%
	Suprapygal 2 & pygal are fused	(3) 5%
	Suprapygal 1 splits diagonally into 2 plates	(4) 6%
	Pygal splits longitudinally into 2 plates	(1) 2%

[1] Shell anomaly categories are taken from Cherepanov (1994, 1997b).

[2] Numbers in parentheses refer to the absolute frequency of a given anomaly in a locality.

diagnosed in two specimens of *M. leprosa*, one from Morocco (USNM 0211407) and the other from Spain (USNM 0211406). In both cases, the recorded anomaly was a longitudinal split of neural 8, similar to the one found in the *M. caspica* population from the Jordan Valley. The presence of this anomaly in other species emphasizes the fact that it is not exclusive to *M. caspica*. In addition, it highlights the necessity of analyzing anomalies at the population rather than the individual level to establish whether an anomaly is repetitive and thus an effective identifying marker of distinct populations.

Shell anomaly in Mauremys caspica at Gesher Benot Ya'aqov

The disarticulated and often fragmented condition of the bony plates from the GBY turtles reduced the potential to identify shell anomalies. Nevertheless, a single anomalous neural plate was discovered. The plate is a complete right half of neural 8, split longitudinally along its anterior/posterior axis (Figure 4). The medial margin of the neural is naturally serrated by a suture, which indicates that the eighth neural was not broken but developed naturally into two separate plates. The dorsal surface of this neural bears a sulcus created by the fifth vertebral keratinous scute, but the ventral surface lacks the vertebral centrum. Hence, the missing centrum must have been part of the left half of the doubled neural. This anomaly is identical to the one most commonly found in the present-day population of *M. caspica* from the Jordan Valley. It is worth noting that out of 20 neural plate fragments that were discovered in GBY, two were identified as neural 8 plates, and one of these was anomalous. Although one cannot rule out the possibility that this anomaly represents an exceptional phenomenon, it would be highly unusual to find one in such a small sample. The identification of a similar anomaly in the sister taxon *M. leprosa* implies that the random occurrence of a longitudinal split is possible. Yet the likelihood of finding this anomaly in the paleontological record should increase proportionally with its abundance in the fossil population. In other words, the discovery of this anomaly, despite the small sample size, suggests its profusion in the ancient turtle population of GBY. Furthermore, the absence of this anomaly in northern populations of *M. caspica* further suggests that its presence in the Jordan Valley populations provides a reliable marker of population continuity.

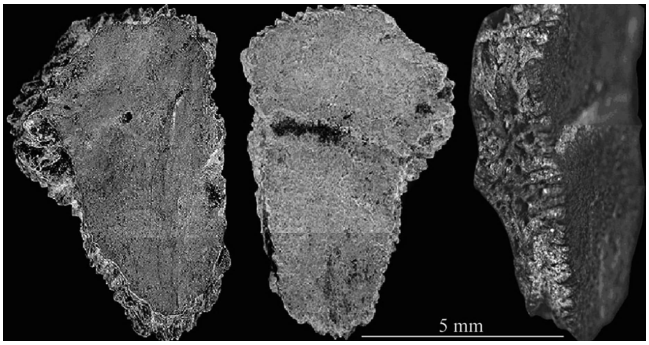

Figure 4. The anomalous longitudinal split of neural 8 in a fossil specimen from GBY. The same bony plate is viewed ventrally (left), and dorsally (center). An additional lateral view (right) shows the medially sutured margin of the scute.

Discussion

Mauremys caspica at Gesher Benot Ya'aqov

Fossil shell remains of *Mauremys* are found in western Asia as early as the Late Miocene (Baynunah Formation, Emirate of Abu Dhabi) (de Lapparent de Broin & van Dijk 1999). However, the earliest appearance of *Mauremys caspica* is at the Middle Pleistocene site of GBY.

Two subspecies of *M. caspica* are recognized: *M. c. rivulata* occurs from southeastern Europe to the eastern borders of the Mediterranean Sea as far south as Israel, and *M. c. caspica* occurs from Transcaucasia in the north to Anatolia, Iraq, and Iran in the east and Saudi Arabia in the south (Busack & Ernst 1980). *M. leprosa* is a sister taxon to *M. caspica* (Merkle 1975); its geographic boundaries include the western shores of the Mediterranean Sea from Spain and Portugal in the north to Senegal in the south and Libya in the east. Busack & Ernst (1980) demonstrated that, despite their disjunct distribution, the phenetic similarity between *M. c. rivulata* and *M. leprosa* is greater than the similarity between *M. c. caspica* and *M. c. rivulata*.

They attribute this similarity to the retention of the ancestral morphotype since the Pliocene due to similar climatic conditions. This interpretation must be questioned, because *Mauremys* fossils from ʻUbeidiya predate the presence of *M. c. rivulata* in the region (Haas 1966). The ʻUbeidiya *Mauremys* remains date to the Early Pleistocene (Tchernov 1987) and the earliest fossils clearly assigned to *M. caspica* from GBY date to the Middle Pleistocene (Verosub et al. 1998; Goren-Inbar et al. 2000). Busack & Ernst (1980) adopt a climatic explanation to account for the differences between the *M. caspica* subspecies. *M. leprosa* and *M. c. rivulata* inhabit Mediterranean climatic regions with more moderate temperatures and a shorter dry season, whereas *M. c. caspica* resides in arid regions with erratic temperatures and fluctuating precipitation. The comparative collection used for the analysis of the fossil remains from GBY consists only of *M. c. rivulata* specimens, yet the resemblance between the shell morphology of the fossil and present-day *M. caspica* is indisputable. Nonetheless, the assignment of the GBY *M. caspica* fossil remains to *M. c. rivulata* does not exclude the possible presence of *M. c. caspica* at the site. *M. c. rivulata* and *M. c. caspica* prefer different climates but cannot be distinguished using morphological criteria alone. Hence, environmental reconstructions based on the presence of *M. caspica* remains should not be undertaken without evidence for population continuity. The presence of unique shell anomalies is currently the only available measure for such a determination.

Differentiation of populations using shell anomalies

Numerical and morphological variation in the turtle shell is common in both the keratinous and osseous components. A sample of freshwater *Trachemys scripta* turtles served as a model to test the hypothesis that the morphology and/or number of anomalies in the carapace segments can differentiate populations of a single species. As previous discussion has already shown, the comparison of four populations of *T. scripta* provides support for this hypothesis. At least two of the populations (Rayville and Wheeler Reservoir) can be distinguished from other populations of the same species based on unique shell anomalies. These results support Zangerl's (1969) argument regarding anomalies in the shell's external keratinous layer. Based on his survey of multiple species and subspecies, Zangerl concluded that anomalies represent the phenotypic expression of genotypic variation.

The use of *Trachemys scripta* as a comparative model for *Mauremys caspica* provides evidence for one of the two criteria necessary to support the population-continuity hypothesis. Direct comparison between different populations of *Mauremys caspica* was not possible for this study because of the absence of comparative material. Published data on shell variation in northern populations of *Mauremys caspica* (Cherepanov 1994), however, show the absence of the divided eighth neural, which is common in the Jordan Valley population. The presence of this anomaly in the Jordan Valley population and its absence in a northern population of *M. caspica* provide a tentative tool to distinguish between the two populations.

Shared shell anomaly and genetic continuity in fossil and present populations

The second criterion needed to support the population-continuity hypothesis is the presence of shared variation in the shells of both fossil and present-day populations of a species. The shared double 8th neural in both fossil and recent populations tentatively supports the continuous presence of the *M. caspica* population in the Jordan Valley. The presence of this neural condition in two temporally distant populations occupying the same restricted geographic boundary suggests a direct hereditary link between the past and present populations. This discovery is significant given the chronological gap of about 790 Ka between the two populations. Since the present subspecies found in the region is assigned to *M. c. rivulata*, it is concluded here that the GBY fossils are also *M. c. rivulata*.

Paleoenvironmental implications

In Israel, two major factors limit the geographic distribution of *M. caspica*: the presence of permanent water bodies, and water salinity. When the water source is intermittent, *M. caspica* is forced to aestivate in the mud (Ernst & Barbour 1989:171). Aestivation, however, can occur only for short periods, since freshwater turtles have a relatively permeable skin to facilitate a high rate of gas exchange (Feder & Burggren 1985), and permeability accelerates dehydration. The population density of *M. caspica* decreases in direct correlation with increases in water salinity (Sidis 1983:33). Freshwater turtles of the sister taxon *Mauremys leprosa* can adjust their osmoregulation to tolerate seawater for a limited period of time (Schoffeniels & Tercafs 1966). Nevertheless, the adaptation of freshwater reptiles to estuarine and marine habitats requires a series of behavioral, anatomical, and physiological alterations (Dunson & Mazzotti 1989), none of which are known to exist in the genus *Mauremys*. *M. caspica* is thus restricted to low-salinity environments. The species favors permanent, slow-moving or standing water habitats in which water depth does not normally exceed one meter. Adapted to benthic foraging, *M. caspica* prefers water bodies that have soft muddy bottoms, rich in water plants and detritus (Sidis 1983).

Assuming that the environmental factors influencing the distribution of modern populations of *Mauremys caspica* are similar to those for the GBY fossil population, these conditions can be used to reconstruct the paleoenvironment at GBY.

Temporal continuity in the upper Jordan Valley *M. caspica* population means that tectonic and volcanic events did not destabilize the freshwater ecosystem despite the region's long and active geological history (Belitsky 2002; Heimann & Ron 1993). Instead, freshwater lakes and marshes must have existed in the basin throughout the entire period (Horowitz 1973; Rosental et al. 1989). Likewise, the last major period of volcanic activity that deposited sediments in the upper Jordan Valley basin (Yarda Basalt, ca. 800–900 Ka; Heinmann & Ron 1993) must predate the establishment of the GBY freshwater turtle population. Unlike the lower Jordan Valley, there are no indications of events that could have increased water salinity and driven the local turtle population to extinction. Furthermore, the results of this research indicate that tectonic activity since prior to the occupation of GBY could not have formed a closed basin (playa lake) that blocked water drainage and increased mineral precipitation through the high evaporation rates in the upper Jordan Valley.

The Jordan Valley is bordered laterally by the Central Mountain Ridge in the west and by the Golan Heights and the Trans-Jordanian Plateau in the east. The Central Mountains lack permanent water sources that are essential for the survival of freshwater turtles, and therefore create a buffer zone that divides and isolates the Jordan Valley *M. caspica* population from that of the Mediterranean seashore (Sidis 1983). It is possible that periodic deterioration of environmental conditions might have forced the distribution of the population towards the freshwater springs that surround the Jordan Valley. However, spring habitats are nutrient-poor and are therefore unsuitable for supporting stable reproductive populations of freshwater turtles. Thus, it is unlikely that such a large-scale shift occurred, as only a fraction of the population could have survived such detrimental events. The isolation of small populations at spring habitats would also have created genetic bottlenecks that would most likely have winnowed out the expression of the anomaly.

The validity of this reconstruction is corroborated by the stratigraphy of lakeshore deposits (Feibel et al. 1998; Goren-Inbar et al. 2000), the preservation of shallow water vegetation (Melamed 1997; Kislev et al. n.d.), and the geochemistry of mollusc shells from the GBY formation (Rosental et al. 1989). The geostratigraphy of GBY indicates cyclical fluctuations in water levels as indicated by alternations in the deposition of fluvial conglomerates and lacustrine fine sediments. These fluctuations presumably resulted from cyclical alterations in the earth's orbital motion (Feibel et al. 1998; Goren-Inbar et al. 2000). The continuous presence of *M. caspica* in the upper Jordan Valley indicates that these climatic changes were moderate and never had devastating effects on the turtle population.

The upper Jordan Valley provided an important route for hominid dispersal through the Levantine Corridor. The continuous presence of freshwater turtle populations serves as reliable evidence for the continuous presence of complex freshwater ecosystems, which secured human migrations throughout the Pleistocene.

Conclusions

The occurrence of *Mauremys caspica* turtles is thus another piece of evidence demonstrating the existence of a freshwater lakeshore and marshland environment at GBY. The discovery of a shell anomaly shared by fossil and present-day populations of *M. caspica* in the same geographic region supports a population-continuity hypothesis. According to this hypothesis, the same turtle population has occupied the upper Jordan Valley since the Pleistocene due to environmental stability. The anomalous longitudinal split of the 8th neural bony plate shared by fossil and recent turtle populations in the upper Jordan Valley is as yet unknown in northern populations of the species. This study has also demonstrated how populations of a single species can be distinguished from one another based on differences in the pattern of their shell anomalies.

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References

Bar-Yosef, O. & Goren-Inbar, N. (1993). *The Lithic Assemblages of 'Ubeidiya.* Qedem 34. Jerusalem: Hebrew University.

Belitzky, S. (2002). The structure and morphotectonics of the Gesher Benot Ya'aqov area, northern Dead Sea Rift, Israel. *Quaternary Research* **58**, 372–380.

Bourn, D. & Coe, M. J. (1979). Features of tortoise mortality and decomposition on Aldabra. *Philosophical Transactions of the Royal Society, Series B: Biological Sciences* **286**, 189–193.

Busack, S. D. & Ernst, C. H. (1980). Variations in Mediterranean populations of *Mauremys* Gray 1869 (Reptilia, Testudines, Emydidae). *Annals of Carnegie Museum* **49**, 251–264.

Cherepanov, G. O. (1989). New morphologenetic data on the turtle shell: Discussion on the origin of the horny and bony parts. *Studia Geologica Salamanticensia* **3**, 9–24.

Cherepanov, G. O. (1994). Anomalies of bony carapace in turtles. *Zoologicheskii Zhurnal* **73**, 68–78.

Cherepanov, G. O. (1997a). The origin of the bony shell of turtles as a unique evolutionary model in reptiles. *Russian Journal of Herpetology* **4**, 155–162.

Cherepanov, G. O. (1997b). Variability of the bony shell in turtles and morphogenetic causes for abnormalities. *Journal of Morphology* **232**, 241.

De Lapparent de Broin, F. & van Dijk, P. P. (1999). Chelonia from the late Miocene Baynunah Formation, Emirate of Abu Dhabi, United Arab Emirates: Palaeogeographic implications. In (P. J. Whybrow & A. Hill, Eds.) *Fossil Vertebrates of Arabia*. New Haven: Yale University Press, pp. 136–162.

Dodd, K. C. (1995). Disarticulation of turtle shells in northern-central Florida: How long does a shell remain in the woods? *American Midland Naturalist* **134**, 378–387.

Dunson, W. A. & Mazzotti, F. J. (1989). Salinity as a limiting factor in the distribution of reptiles in Florida Bay: A theory for the estuarine origin of marine snakes and turtles. *Bulletin of Marine Science* **44**, 229–244.

Ernst, C. H. & Barbour, R. W. (1989). *Turtles of the World*. Washington, DC: Smithsonian Institution Press.

Ernst, C. H., Lovich, J. E. & Barbour, R. W. (1994). *Turtles of the United States and Canada*. Washington, DC: Smithsonian Institution Press.

Feder, M. E. & Burggren, W. W. (1985). Skin breathing in vertebrates. *Scientific American* **253**, 126–142.

Feibel, C. S., Goren-Inbar, N., Verosub, K. L. & Saragusti, I. (1998). Gesher Benot Ya'aqov, Israel: New evidence for its stratigraphic and sedimentologic context. *Journal of Human Evolution* **34**, A7.

Fritz, U. (1989). Does or did the European Pond Turtle, *Emys orbicularis* (Reptilia: Testudines), occur in Israel? *Israel Journal of Zoology* **36**, 81–84.

Fritz, U., Baran, I., Budak, A. & Amthauer, E. (1998). Some notes on the morphology of *Emys orbicularis* in Anatolia, especially on *E. o. luteofusca* and *E. o. colchica*, with the description of a new subspecies from southeastern Turkey. In (U. E. A. Fritz, Ed.) *Proceedings of the EMYS Symposium 96*. Dresden: Deutche Gesellschaft für Herpetologie und Terrarienkunde, pp. 103–121.

Gadow, H. (1899). Orthogenetic variation in the shells of Chelonia. *Willey's Zoological Results* **Part III**, 207–222.

Gaffney, E. S. (1990). The comparative osteology of the Triassic turtle Proganochelys. *Bulletin of American Museum of Natural History* **194**, 1–263.

Gaffney, E. S. & Meylan, P. (1988). A phylogeny of turtles. In (M. J. Benton, Ed.) *The Phylogeny and Classification of the Tetrapods*. Oxford: Clarendon Press, pp. 157–219.

Gilbert, S. F., Loredo, G. A., Brukman, A. & Burke, A. C. (2001). Morphogenesis of the turtle shell: The development of a novel structure in tetrapod evolution. *Evolution and Development* **3**, 47–58.

Goren-Inbar, N., Belitzky, S., Goren, Y., Rabinovich, R. & Saragusti, I. (1992). Gesher Benot Ya'aqov – the "Bar": An Acheulian assemblage. *Geoarchaeology* **7**, 27–40.

Goren-Inbar, N., Lister, A., Werker, E. & Chech, M. (1994). A butchered elephant skull and associated artifacts from the Acheulian site of Gesher Benot Ya'aqov, Israel. *Paléorient* **20**, 99–111.

Goren-Inbar, N. & Saragusti, I. (1996). An Acheulian biface assemblage from Gesher Benot Ya'aqov, Israel: Indications of African affinities. *Journal of Field Archaeology* **23**, 15–30.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–947.

Goren-Inbar, N., Sharon, G., Melamed, Y. & Kislev, M. (2002a). Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *Proceedings of the National Academy of Sciences USA* **99**, 2455–2460.

Goren-Inbar, N., Werker, E. & Feibel, C. S. (2002b). *The Acheulian Site of Gesher Benot Ya'aqov, Israel, 1. The Wood Assemblage*. Oxford: Oxbow Books.

Hartman, G. (2001). *Ecology, Morphometry and Taphonomy of the Freshwater Turtle Mauremys caspica rivulata in the Jordan Valley Today, and 780 Kya at the Site of Gesher Benot Ya'akov, Israel.* Unpublished M.A. Thesis, Hebrew University of Jerusalem.

Heimann, A. & Ron, H. (1993). Geometric changes of plate boundaries along part of the northern Dead Sea transform: Geochronologic and paleomagnetic evidence. *Tectonics* **12**, 477–491.

Hoffstetter, R. & Gasc, J.-P. (1969). Vertebrae and ribs of modern reptiles. In (C. Gans, A. d. A. Bellaivs & T. S. Parson, Eds.) *Biology of the Reptilia, Vol. 1*. London: Academic Press, pp. 201–310.

Holman, J. A. (1998). *Pleistocene Amphibians and Reptiles in Britain and Europe*. New York: Oxford University Press.

Horowitz, A. (1973). Development of the Hula Basin, Israel. *Israel Journal of Earth Sciences* **22**, 107–139.

Kazmaier, R. T. & Robel, R. J. (2001). Scute anomalies of ornate box turtles in Kansas. *Transactions of the Kansas Academy of Science* **104**, 178–182.

Lynn, G. W. (1937). Variations in scutes and plates in the box turtle, *Terrapene carolina. American Naturalist* **71**, 421–426.

Lynn, G. W. & Ullrich, M. C. (1950). Experimental production of shell abnormalities in turtles. *Copeia* **4**, 253–262.

Melamed, Y. (1997). *Reconstruction of the Landscape and the Vegetation Diet at Gesher Benot Ya'aqov Archaeological Site* *in the Lower Paleolithic Period.* Unpublished M.Sc. Thesis, Bar-Ilan University, Ramat-Gan, Israel.

Merkle, D. A. (1975). A taxonomic analysis of the *Clemmys* complex (Reptilia: Testudines) using starch gel electrophoresis. *Herpetologica* **31**, 162–166.

Newman, H. H. (1906). The significance of scute and plate "abnormalities" in Chelonia. *Biological Bulletin* **10**, 68–114.

Parker, G. H. (1901). Correlated abnormalities in the scutes and bony plates of the carapace of the sculptured tortoise. *American Naturalist* **35**, 17–24.

Parmenter, R. R. & Avery, R. A. (1990). The feeding ecology of the slider turtle. In (J. W. Gibbons, Ed.) *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 257–266.

Pritchard, P. C. H. (1979). *Encyclopedia of Turtles*. Neptune, NJ: TFH Publications.

Rhodin, A. G. J., Mittermeier, R. A. & Hall, P. M. (1993). Distribution, osteology and natural history of the Asian giant softshell turtle, *Pelochelys bibroni*, in Papua, New Guinea. *Chelonian Conservation and Biology* **1**, 19–30.

Rosental, Y., Katz, A. & Tchernov, E. (1989). The reconstruction of Quaternary freshwater lakes from the chemical and isotopic composition of gastropod shells: The Dead Sea Rift, Israel. *Palaeogeography, Palaeoclimatology, Palaeoecology* **74**, 241–253.

Schoffeniels, E. & Tercafs, R. R. (1966). Adaptation d'un reptile marin, *Caretta caretta* l. à l'eau douce et d'un reptile d'eau douce, *Clemmys leprosa* l. à l'eau de mer. *Extrait des Annales de la Société Royale Zoologique de Belgique* **96**, 1–8.

Seidel, M. E. & Jackson, D. R. (1990). Evolution and fossil relationships of slider turtles. In (J. W. Gibbons, Ed.) *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 68–73.

Shaffer, H. B., Meylan, P. & McKnight, M. L. (1997). Tests of turtle phylogeny: Molecular, morphometrical, and paleontological approaches. *Systematic Biology* **46**, 235–268.

Sharon, G. (2000). *Acheulian Basalt Tools of Gesher Benot Ya'aqov: Experimental and Technological Study.* Unpublished M.A. Thesis, Hebrew University of Jerusalem.

Sidis, I. (1983). *Ecology of the Caspian Terrapin (Mauremys caspica rivulata) in Polluted and Unpolluted Habitats in Israel.* Unpublished M.Sc. Thesis, Tel Aviv University.

Smith, M. H. & Scribner, K. T. (1990). Population genetics of the slider turtle. In (J. W. Gibbons, Ed.) *Life History and Ecology of the Slider Turtle*. Washington, DC: Smithsonian Institution Press, pp. 74–81.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. New York: Freeman.

Tchernov, E. (1987). The age of the 'Ubeidiya Formation, an Early Pleistocene hominid site in the Jordan Valley. *Israel Journal of Earth Sciences* **36**, 3–30.

Verosub, K. L., Goren-Inbar, N., Feibel, C. S. & Saragusti, I. (1998). Location of the Matuyama/Brunhes boundary in the Gesher Benot Ya'aqov archaeological site. *Journal of Human Evolution* **34**, A22.

Zangerl, R. (1969). The turtle shell. In (C. Gans, Ed.) *Biology of the Reptilia, Vol. 1*. London and New-York: Academic Press, pp. 311–339.

Zangerl, R. & Johnson, R. G. (1957). The nature of shield abnormalities in the turtle shell. *Fieldiana Geology* **10**, 341–362.

Chapter VI

Early Hominid Subsistence in the Levant: Taphonomic Studies of the Plio-Pleistocene ʻUbeidiya Formation (Israel) – Evidence from ʻUbeidiya II-24

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Abstract

This paper reports the results of a taphonomic faunal analysis of the Plio-Pleistocene ʻUbeidiya Formation (Israel), focusing on ʻUbeidiya layer II-24. The role of hominids in assemblage formation is indicated by the presence of stone artifacts, as well as by cut-marks on bones. Evidence for marrow processing is lacking. The faunal assemblage from layer II-24 is representative of other assemblages from the ʻUbeidiya Formation from which comparable results have been obtained. The evidence from layer II-24 is discussed in a broader context, and it is concluded that hunting of medium-sized animals was probably among the subsistence strategies of Early Pleistocene Levantine hominids.

Introduction

Evidence obtained using different approaches, including archaeozoology (e.g., Gaudzinski 1996), isotopic studies (Bocherens et al. 2001; Richards et al. 2001), and lithic analyses (Shea 1997), suggests that European late Middle and Upper Pleistocene hominids were competent hunters. This hypothesis is underscored by the presence of numerous spears discovered at the German site of Schöningen, indicating that the hunting way of life was already practiced by the earliest European inhabitants north of the Pyrenees and Alps half a million years ago (Roebroeks 2001; Thieme 1997).

In contrast, many researchers hold that scavenging, at least of larger animals, constituted a major component of the behavioral repertoire of our earliest Plio-Pleistocene African ancestors (Blumenschine 1995; Lupo 1998). Given the possible differences in subsistence strategies, as inferred from the European Middle and Upper Pleistocene and the Plio-Pleistocene African records, sites located in time and space between the two records mentioned might shed light on the question of when and where large-mammal hunting emerged. The Israeli ʻUbeidiya Formation represents one of the very rare cases where such a study can be performed.

The present paper first introduces the ʻUbeidiya Formation. A general overview of the faunal assemblages analyzed from this site is given, followed by a detailed description of the analysis of the faunal material from layer II-24. The results are discussed in a broader context.

The ʻUbeidiya Formation and its setting

The ʻUbeidiya Formation is located in the Jordan Valley (Israel), approximately 3.5 km south of Lake Kinneret. The formation represents a tectonic anticline with undulations and faults. The sediments are tilted up to 80° and exposed over an area of ca. 1 km^2 (Picard & Baida 1966; Bar-Yosef & Goren-Inbar 1993).

Four major depositional cycles can be distinguished within the formation: lower limnic and fluvial deposits and upper limnic and fluvial deposits. These sediments reflect temporal changes in an environment controlled by geomorphological processes in which the delta of an ephemeral stream debouched into a freshwater lake.

The majority of archaeological sites at ʻUbeidiya stem from the ca. 30-m-thick lower fluvial cycle, which displays clay, clastic conglomerates, clayey and chalky marls, silt, and basaltic sands. Whereas the western part of the cycle represents fluvial deposits, the eastern part represents swamps (Picard & Baida 1966; Bar-Yosef & Goren-Inbar 1993). Throughout the depositional cycle, paleosol genesis can be observed (Feibel, personal communication, 2001).

Geological and biostratigraphical evidence indicates that the ʻUbeidiya Formation dates between 1.4 and 1.0 Ma. Geological evidence suggests a *terminus post quem* of ca. 2 Ma, the estimated age of the underlying Erq el-Ahmar Formation, and a *terminus ante quem* of ca. 0.80 Ma, based on the overlying K-Ar-dated Yarmuk basalt. The fauna shows affinities to those known from the European Villafranchian, pointing to an age of approximately 1.4 Ma (Tchernov 1986, 1987).

Excavations at ʻUbeidiya started in 1960 and continued until 1974. Excavations were initially directed by M. Stekelis and later by O. Bar-Yosef and E. Tchernov (Stekelis et al. 1969; Bar-Yosef & Tchernov 1972; Bar-Yosef & Goren-Inbar 1993). More recent work was started in the early 1990's by an Israeli-French-American team (Guérin et al. 1996) and completed by an Israeli-German-American team in the late 1990's.

During these years, a total of 80 archaeological horizons with stone artifacts and bones were discovered (Guérin et al. 1996; Bar-Yosef & Goren-Inbar 1993). For the majority of the archaeological horizons, stone artifacts and bones were in primary context.

A number of important studies have been undertaken at ʻUbeidiya so far, including analysis of stone artifacts (Bar-Yosef & Goren-Inbar 1993) and paleontological analysis of large mammal species (Guérin et al. 1993; Martinez-Navarro 1999, 2000; Tchernov 1973, 1980, 1986).

Materials and methods

Taphonomic studies of faunal remains from the ʻUbeidiya Formation were undertaken. A total of 17 assemblages were analyzed (I-15 LF, I-15/16, I-16, I-26b1/b2, K29VB, II-23, II-23/24, II-24, II-26, II-36, III-22a, III-22b inf., III-22c, III-22d, III-22d-base, III-22e. inf., III-22e sup.) (Table 1). These assemblages were unearthed during both the old and the new excavations at ʻUbeidiya. Their sedimentary contexts were conglomerates, clays and coquinas (i.e., shell-rich deposits) of varying thickness. The sediments represent shoreline deposits, paleosols, wadi beds, and swamps.

The size of these assemblages differs enormously. Individual assemblages of bones may comprise from as many as 1600 specimens to as few as six. The same applies to the number of artifacts.

Studies focused on the particular assemblages mentioned above, in which the preservation of the remains allowed recognition of the traces necessary to reconstruct the taphonomic history of the bones. These traces include cut-marks made by stone tools, carnivore gnawing damage and punctures, and striations and percussion-marks resulting from hominid marrow processing.

Taphonomic analysis included detailed description of each specimen and comparative study of skeletal frequencies across taxa. Taxonomic determination is based on species identifications made in the 1980's (Tchernov 1986) and revisions thereof (Martinez-Navarro 1999, 2000; Pfeiffer 1999; Guérin et al. 1993). On average, half to one-third of the faunal remains within each assemblage were identified to taxon.

In cases where exact taxonomic determination was not possible, epiphyses and shaft fragments were assigned to approximate animal size/weight classes, as defined by Bunn (1997) (Table 2). Where possible, ontogenetic age and sex determination was undertaken.

The qualitative and quantitative composition of the faunal assemblages were checked against structural bone density (Lyman 1994), bone volume (Behrensmeyer 1975), form mediation (Frostick and Reed 1983), and hydraulic transport potential (Behrensmeyer 1975).

Fragmentation was studied by three-dimensional analysis of each bone, as well as qualitative, quantitative, and metric documentation of the observed breakage patterns. The nature and quantity of all surface

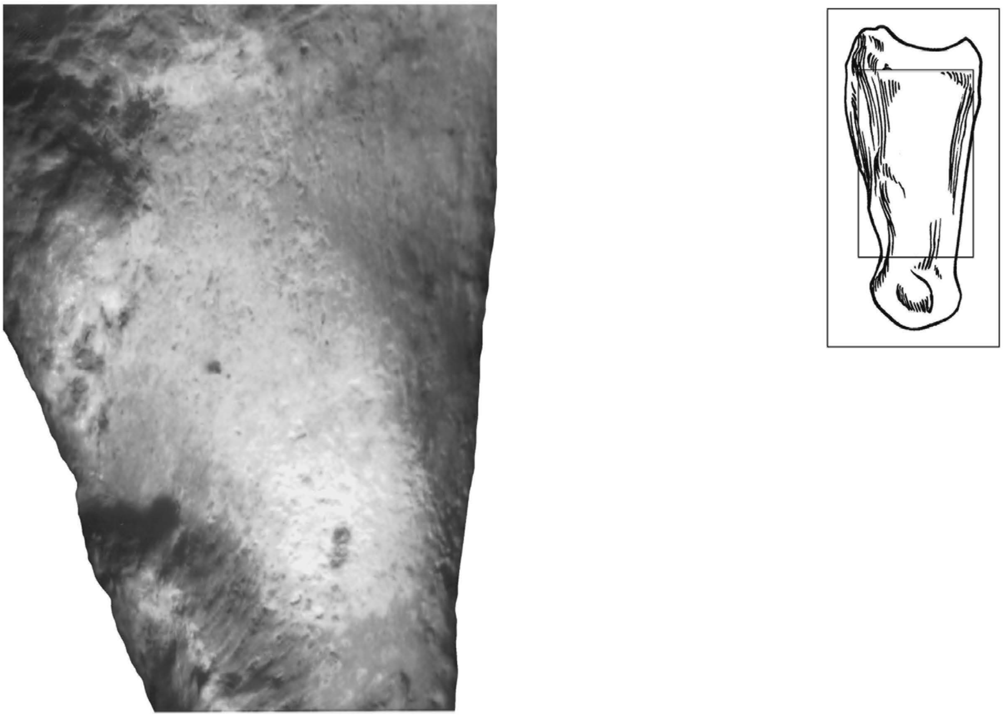
Table 1. Summary of analyzed faunal assemblages from sites of the 'Ubeidiya Formation.

Site	Years Excavated	Sediment	Thickness of Layer	Paleo-milieu	Area Exposed m^2	N Bones	N Artifacts	N Cut-marked Bones	N Bones w. Conical Impacts
I-15LF/I-16	1963–74	conglomerate on green clay	ca. 30 cm	shoreline	250	1631	1126	2	1
I-26b1/b2	1968–74	conglomerate & sandy clay	25 cm	shoreline	75	90	97	–	–
II-23	1961–63	silty clay lens	ca. 20 cm	paleosol	105	1180	33	2	12
II-24	1961–63	green clay	ca. 2.5 m	paleosol	111	785	327	5	6
II-26	1963–74	conglomerate & sand	ca. 1.2 m	shoreline	28	472	970	1	1
II-36	1963–74	molluscan clay	ca. 40 cm	shoreline/ paleosol	13	608	500	1	1
K29/30VB	1969–70	wadi sediments	ca. 24 cm	wadi bed	3	56	432	–	–
III-22a	1997–99	green clay	ca. 35 cm	paleosol	14	196	83	–	–
III-22b inf.	1997–99	green clay	10–20 cm	paleosol	14	60	81	–	–
III-22b sup.	1997–99	coquina	ca. 30 cm	lacustrine	14	6	2	–	–
III-22c	1997–99	green clay	ca. 1 m	paleosol	13	65	161	–	–
III-22d	1997–99	green clay w. molluscs	ca. 50 cm	swamp	22	594	113	2	–
III-22d base	1997–99	red clay	ca. 10 cm	paleosol	6	138	132	2	–
III-22e inf.	1997–99	red clay	ca. 1.2 m	paleosol	22	141	23	1	–
III-22e sup.	1997–99	green vertisol	ca. 50 cm	paleosol	25	77	22	–	7

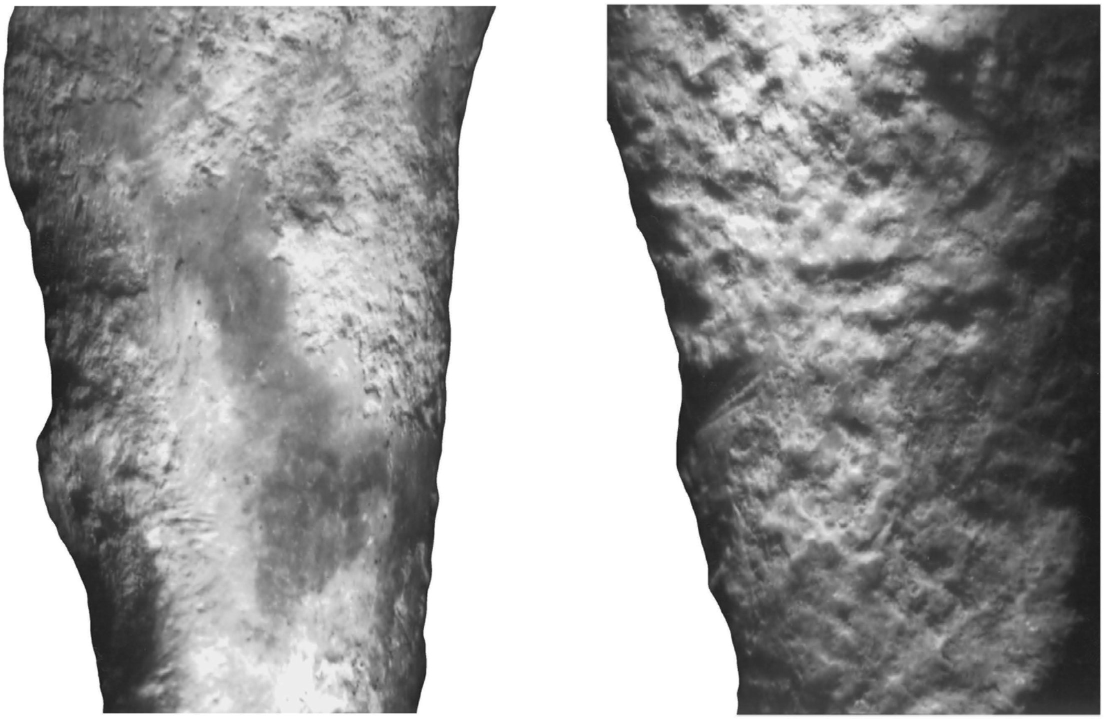
Table 2. Size/weight classes for different taxa of the 'Ubeidiya Formation (after Bunn 1997).

Size/Weight Class	Weight in Kg	Taxa
1	< 23	*Hypolagus brachygnathus, Macaca sylvana, Canis etruscus, Canis (Xenocyon) falconeri, Vulpes* sp., *Lutra* sp., *Pannonictis ardea, Vormela* cf. *peregusna, Lynx* sp., *Felis* sp., *Herpestes* sp., *Hystrix indica*
2	23–114	*Homo* sp., *Megantereon whitei, Panthera gombaszoegensis, Crocuta crocuta, Sus* sp., Cervidae gen. et sp. indet., *Oryx* sp., *Gazella* sp.
3	114–205	*Kolpochoerus olduvaiensis*
	205–340	*Equus* cf. *altidens*, cf. *Pontoceros* sp., *Hippotragus* sp.
4	340–910	*Ursus etruscus, Praemegaceros verticornis, Pelorovis* sp.
5	> 910	*Hippopotamus behemoth, Hippopotamus gorgops, Stephanorhinus e. etruscus,* Giraffidae gen. indet.
6	> 2737	*Mammuthus meridionalis*

modifications originating from non-biotic agents (e.g., abrasion, climatically induced weathering, striations, and deposits on bone surfaces) were analyzed using a stereoscopic microscope and an image analyzer with magnifications between 0.7x and15x. The same applied to modifications induced by biotic agents such as plants, rodents, carnivores, and hominids (Gaudzinski n.d.). Three categories were generated to describe the state of bone preservation within the assemblage (Figure 1). Category 1 includes bones with intact surfaces. Category 2 is characterized by only partial bone surface preservation. Bones attributed to category 3 lack their original surface.



Preservation 1



Preservation 2

Preservation 3

Figure 1. 'Ubeidiya layer II-24, differing stages of bone preservation demonstrated for Phalanx 2 of Cervidae gen. et sp. indet.

Layer II-24 of the 'Ubeidiya Formation

The results of taphonomic analysis of the layer II-24 faunal remains will be presented here. These results proved to be representative of other bone assemblages from the 'Ubeidiya Formation. such as II-23, II-36 and III-22d.

Layer II-24 was described by Picard & Baida (1966) as a grayish-brown clay with white chalk and occasional gypsum concretions that was altered by paleosol genesis (Feibel, personal communication, 2001). Layer II-24 is 2.50 m thick.

The lower part of this horizon especially is rich in gastropods, and malacological studies have enabled a paleoecological reconstruction (Bar-Yosef & Tchernov 1972). The mollusc fauna is characterized by a dominance of *Melanopsis praemorsa*, a low proportion of *Theodoxus jordani*, and *Unio* of below 1%, indicating shallow, swampy water surrounded by dense vegetation (Bar-Yosef & Tchernov 1972:18).

Layer II-24 was excavated in 1961–1963 by M. Stekelis (1966). Renewed excavations by O. Bar-Yosef and E. Tchernov were undertaken between 1968 and 1974. During these years, 111 m² were uncovered. Excavation techniques included three-dimensional documentation of archaeological remains as well as sediment sieving.

Layer II-24 yielded 327 stone artifacts, the majority of which were simple flakes (N=220). In addition, numerous choppers (N=30) were recorded (Bar-Yosef & Goren-Inbar 1993).

The faunal assemblage

The faunal assemblage of layer II-24 comprised 785 specimens, of which 380 could be taxonomically determined (Table 3). A further 351 specimens were attributed to size/weight classes. In addition, there were 54 unidentifiable bone fragments, as well as numerous fragments smaller than 1 cm that could not be identified either and were not included in the analysis.

Within the fauna, the frequent presence of carnivore species (N=7) is striking. With at least five individuals each, Cervidae gen. et sp. indet. and *Equus* cf. *altidens* are the most common taxa.

Table 3. 'Ubeidiya layer II-24: taxa, NISP, and MNI.

Taxon	NISP	MNI
Hystrix indica	5	2
Hypolagus brachygnatus	15	1
Macaca sylvana	2	1
Ursus etruscus	1	1
Canis etruscus	19	2
Canis (Xenocyon) falconeri	1	1
Vulpes sp.	1	1
Lutra sp.	2	1
Megantereon sp. cf. *Megantereon* cf. *whitei*	1	1
Lynx sp.	1	1
Crocuta crocuta	5	1
Hippopotamus behemoth	62	3
Praemegaceros verticornis	25	2
Cervidae gen. et sp. indet.	148	5
Pelorovis sp.	1	1
Gazella sp.	4	1
cf. *Pontoceros* sp.	5	1
Hippotragini indet. cf. *Hippotragus* sp.	2	1
Stephanorhinus e. etruscus	10	1
Equus cf. *altidens*	70	5
Mammuthus meridionalis	1	1

NISP = Number of identified specimens per taxon.
MNI = Minimum number of individuals.

The skeletal element representation for Cervidae is dominated by teeth and the distal humerus. Remains of juveniles (N=4) representing at least one individual have survived. MNI calculation for adult individuals is based on four right M2 sup.

Among the skeletal elements of horse, teeth and tibia mid-shaft fragments dominate. Bones of juveniles/subadults (N=2) representing at least one individual survived. MNI calculation for adults is based on four P4 inf. dext.

Of interest is the composition of the *Hippopotamus behemoth* sample. *H. behemoth* is mainly represented by tooth fragments (N=43). Among the postcranial remains, carpals and tarsals (N=6), phalanges (N=5), and metapodial fragments (N=4) prevail. The presence of bones from neonatal individuals is remarkable. At least two individuals are represented by these remains, which include an *os ischium* with acetabulum, a proximal humerus, and a metatarsal II sin. (Figure 2).

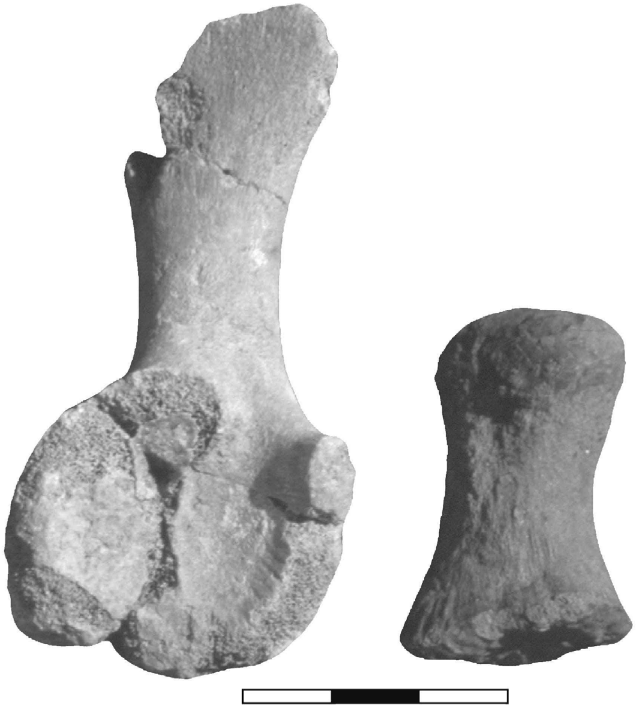


Figure 2. ʻUbeidiya layer II-24, *Hippopotamus behemoth* metatarsus and pelvis from neonatal individuals.

A total of 287 skeletal remains was attributed to size/weight class 2 (Table 2). Skeletal element representation for this class is dominated by elements of the trunk and mid-shaft fragments from all longbones (Table 4). The assemblage is completed by 11 shaft fragments, fragments of a carpal/tarsal bone, 91 longbones, and six metapodials. None of these specimens could securely be attributed to body part.

Table 5 lists the qualitative and quantitative composition of size/weight class 3. In addition to these specimens, 15 longbone fragments were attributed to this class. Size/weight class 3 is dominated by teeth.

With 160 bones, size/weight class 4 is also well represented within the sample. Elements of the trunk occur frequently, as do elements of the autopodium (Table 6). Five skull fragments, five molars from Bovini taxa, fragments of 62 longbones, four metapodials, and two carpal/tarsals, as well as 14 additional bones, were also attributed to this class but could not be included in Table 6.

Table 4. ʻUbeidiya layer II-24: skeletal element representation for size/weight class 2.

Element	NISP	MNE sin.	MNE s/d	MNE dext.	MNE ges.	% MNE
Antler	15	2	13	–	3.0	25.0
Maxilla	22	3	–	3	6.0	50.0
Mandible	35	4	1	5	10.0	83.3
Vertebrae	9	–	9	–	9.0	75.0
Pelvis	3	–	2	–	2.0	16.6
Ribs	6	–	6	–	6.0	50.0
Scapula	4	3	1	–	4.0	33.3
Hum. prox.	–	–	–	–	–	–
Hum. dia.	8	1	6	1	8.0	66.6
Hum. dist.	7	3	–	4	7.0	58.3
Radius prox.	1	–	–	1	1.0	8.3
Radius dia.	12	–	10	2	12.0	100.0
Radius dist.	1	–	–	1	1.0	8.3
Ulna	3	1	1	1	3.0	25.0
MC prox.	3	1	–	2	3.0	25.0
MC dia.	1	1	–	–	1.0	8.3
MC dist.	2	–	2	–	2.0	16.6
Carpal	4	1	1	–	2.0	16.6
Femur prox.	1	–	1	–	1.0	8.3
Femur dia.	10	2	7	1	10.0	83.3
Femur dist.	1	–	–	1	10.0	8.3
Tibia prox.	–	–	–	–	–	–
Tibia dia.	7	–	7	–	7.0	58.3
Tibia dist.	3	–	–	3	3.0	25.0
MT prox.	4	–	–	4	4.0	33.3
MT dia.	1	–	1	–	1.0	8.3
MT dist.	–	–	–	–	–	–
Tarsal	2	2	–	–	2.0	16.6
Calcaneus	3	2	–	1	3.0	25.0
Astragalus	4	1	–	2	3.0	25.0
Phalanx 1	8	3	2	3	8.0	66.6
Phalanx 2	3	2	–	1	3.0	25.0
Phalanx 3	5	2	–	2	4.0	33.3

NISP = number of identified specimens per taxon.
MNE sin. = Minimum number of left elements.
MNE dext. = Minimum number of right elements.
MNE s/d = MNE sin. or dext.
MNE ges. = total MNE.

Bone surface preservation was documented for 697 specimens. Of these, 121 (17.4%) were in stage 1 (original surface intact), 246 (35.2%) in stage 2 (original surface only partially preserved), and 330 (47.3%) in stage 3 (original surface lacking). None of the surface damage evident in these specimens can be attributed to climatically induced weathering, according to criteria developed by

Table 5. ʻUbeidiya layer II-24: skeletal element representation for size/weight class 3.

Element	**NISP**	**MNE sin.**	**MNE s/d**	**MNE dext**	**MNE ges.**	**% MNE**
Maxilla	12	3	–	2	5.0	50.0
Mandible	21	6	–	4	10.0	100.0
Ribs	5	–	5	–	5.0	50.0
Hum. prox.	–	–	–	–	–	–
Hum. dia.	1	–	1	–	1.0	10.0
Hum. dist.	2	1	–	1	2.0	20.0
Radius prox.	–	–	–	–	–	–
Radius dia.	1	–	–	1	1.0	10.0
Radius dist.	2	2	–	–	2.0	20.0
MC prox.	3	1	1	1	3.0	30.0
MC dia.	3	–	2	1	3.0	30.0
MC dist.	–	–	–	–	–	–
Carpal	5	1	1	1	2.0	20.0
Femur prox.	2	–	1	1	2.0	20.0
Femur dia.	1	–	1	–	1.0	10.0
Femur dist.	–	–	–	–	–	–
Tibia prox.	–	–	–	–	–	–
Tibia dia.	4	2	1	1	4.0	40.0
Tibia dist.	1	–	–	1	1.0	10.0
MT prox.	1	–	–	1	1.0	10.0
MT dist.	2	–	2	–	2.0	20.0
Tarsal	1	1	–	–	1.0	10.0
Calcaneus	1	1	–	–	1.0	10.0
Astragalus	1	–	–	1	1.0	10.0
Phalanx 1	4	–	4	–	4.0	40.0
Phalanx 2	1	–	1	–	1.0	10.0
Phalanx 3	1	–	1	–	1.0	10.0

NISP = number of identified specimens per taxon.
MNE sin. = Minimum number of left elements.
MNE dext. = Minimum number of right elements.
MNE s/d = MNE sin. or dext.
MNE ges. = total MNE.

Table 6. ʻUbeidiya layer II-24: skeletal element representation for size/weight class 4.

Element	**NISP**	**MNE sin.**	**MNE s/d**	**MNE dext.**	**MNE ges.**	**% MNE**
Maxilla	4	2	1	–	4.0	22.2
Mandible	4	2	1	1	4.0	22.2
Vertebrae	18	–	18	–	18.0	100.0
Pelvis	3	–	3	3	3.0	16.6
Ribs	4	–	4	–	4.0	22.2
Hum. prox.	–	–	–	–	–	–
Hum. dia.	7	1	5	1	7.0	38.8
Hum. dist.	1	1	–	–	1.0	5.5
Radius prox.	1	–	–	1	1.0	5.5
Radius dia.	2	–	–	2	2.0	11.1
Radius dist.	–	–	–	–	–	–
MC prox.	–	–	–	–	–	–
MC dia.	3	–	3	–	3.0	16.6
MC dist.	2	–	2	–	2.0	11.1
Carpal	1	–	1	–	10.0	5.5
Femur prox.	–	–	–	–	–	–
Femur dia.	2	–	2	–	20.0	11.1
Femur dist.	–	–	–	–	–	–
MT prox.	3	1	–	2	3.0	16.6
MT dist.	1	1	–	–	1.0	5.5
Calcaneus	3	2	–	1	3.0	16.6
Astragalus	4	1	–	3	40.0	22.2
Phalanx 1	1	–	1	–	1.0	5.5
Phalanx 2	2	–	1	1	2.0	11.1
Phalanx 3	2	–	–	2	2.0	11.1

NISP = number of identified specimens per taxon.
MNE sin. = Minimum number of left elements.
MNE dext. = Minimum number of right elements.
MNE s/d = MNE sin. or dext.
MNE ges. = total MNE.

Behrensmeyer (1978). The state of bone surface preservation is independent of taxon and anatomical element.

In order to establish whether the proportional representation of different skeletal elements in the layer II-24 assemblage was affected by their structural bone density, % survivorship values for size/weight classes 2–4, calculated according to Lyman (1994:239), were correlated with density values obtained by photon densitometry of deer bones (Lyman 1994: his Table 7.6) (Table 7). The correlation coefficient is r =0.41 for size/weight class 3 and 0.63 for both size/weight classes 2 and 4. On the basis of these results, it seems plausible to propose at least some degree of density-mediated attrition of bones in layer II-24.

In contrast, correlation between bone volume (Behrensmeyer 1975) and skeletal element representation for size/weight classes 2 and 3 gave only negative and non-significant values of $r = -0.39$ for class 2 and $r = -0.23$ for class 3 (Table 8).

As all elements were documented within the death assemblage, there is no indication if its composition was affected by hydrodynamic transport.

Table 7. Structural bone density of deer bones and % survivorship values for animal size/weight classes 2–4 in ‘Ubeidiya layer II-24 by skeletal element and density scan site (after Lyman 1994: Table 7.6).

Element/Scan Site	Structural Bone Density	% Surv. Class 2	% Surv. Class 3	% Surv. Class 4
Mandible Dn4	0.57	62.5	71.4	40
Atlas At3	0.26	0	0	0
Epistropheus Ax3	0.16	0	0	0
Cervical Ce1	0.19	0	0	0
Thoracic Th2	0.27	0	0	0
Lumbar Lu1	0.29	0	0	0
Pelvis Pu1	0.46	12.5	0	30
Ribs Ri3	0.4	0	0	0
Scapula Sp2	0.49	25	0	0
Humerus Hu2	0.25	0	0	0
Humerus Hu4	0.63	43.7	14.2	10
Radius Ra2	0.62	6.25	0	10
Radius Ra5	0.43	6.25	14.2	0
Ulna Ul2	0.45	18.75	0	0
Metacarpus Mc2	0.69	18.75	21.4	0
Metacarpus Mc6	0.51	12.5	0	20
Femur Fe1	0.41	6.25	14.2	0
Femur Fe6	0.28	6.25	0	0
Tibia Ti2	0.32	0	0	0
Tibia Ti5	0.5	18.75	7.1	0
Metatarsus Mr2	0.65	25	7.1	30
Metatarsus Mr6	0.51	0	14.2	10
Calcaneus Ca2	0.64	18.75	7.1	30
Astragalus As2	0.59	18.75	7.1	40
Phalanx 1 P13	0.57	12.5	11.1	2.5
Phalanx 2 P23	0.35	4.6	2.7	5
Phalanx 3 P31	0.25	6.25	2.7	5

Table 8. Bone volume (cm^3; after Behrensmeyer 1975: Appendix 1) and size/weight classes 2 and 3 in ‘Ubeidiya layer II-24 by skeletal element.

Skeletal Element	Volume *Damaliscus*	% MNE Class 2	Volume *Equus*	% MNE Class 3
Maxilla	3.6	50	–	50
Mandible	3.6	83.3	–	100
Atlas	63	0	139	0
Epistropheus	1.33	8.3	155	0
Cervical	62	8.3	170	0
Thoracic	22.8	33.3	64	0
Lumbar	40	25	49	0
Sacrum	1.25	0	–	0
Scapula	65	33.3	100	0
Hum. prox.	129	0	168	0
Hum. dist.	94	58.3	150	20
Rad. prox.	65	8.3	170	0
Rad. dist.	84	8.3	147	20
MC prox.	60	25	82	30
MC dist.	58	16.6	90	0
Carpal	16.2	16.6	10.4	20
Femur prox.	128	8.3	325	20
Femur dist.	168	8.3	299	0
Tibia prox.	154	0	235	0
Tibia dist.	96	25	168	10
MT prox.	61	33.3	68	10
MT dist.	58	0	68	20
Tarsal	16.2	16.6	14.8	10
Calcaneus	36	25	87	10
Astragalus	24	25	63	10
Phalanx 1	17.9	66.6	48	40
Phalanx 2	8.1	25	–	10
Phalanx 3	7.9	33.3	20	10

For further description of the faunal assemblage, metrical analysis of bones and bone fragments was undertaken; 554 faunal elements were included in the analysis. Certain elements, such as tooth fragments, were excluded, as it seems likely that most teeth, especially those of hippo, were still intact when they were first buried.

Analysis shows that the length of the majority of bones is between 2 and 6 cm, their breadth about 4 cm, and their thickness between 0.5 and 2.5 cm.

For analysis of shape, indices were calculated from three-dimensional measurements that were then plotted in a scatterplot (Frostick & Reed 1983). The diagram is subdivided into four sections representing blade-, rod-, disc-, and sphere-shaped specimens. Bones from layer II-24 scatter in all sectors of the diagram and only a very slight predominance of blade- and disc-shaped elements is evident, indicating that shape probably did not represent a filter that affected the composition of the bone assemblage.

The overwhelming majority of bones are characterized by rectangular breakage probably resulting from sediment compression. Only 12.2% of the metrically analyzed material (N=554) is characterized by spiral fractures.

Conically induced impacts were documented on only six humerus and femur fragments, of which two were attributed to size/weight class 2, three to class 3, and one to class 4. Four of these specimens show more than one impact located next to, or opposed to, each other.

Biotically induced modifications on bones were documented. That bones were affected by carnivores is evident from 21 specimens with gnawing marks. These bones include calcanei, distal humeri, tibiae, femora, and metapodials attributed to animals of size/weight classes 2 to 4. Digested bones were not observed. Five coprolites, which most plausibly originate from the spotted hyena, *Crocuta crocuta*, underscore the involvement of carnivores in the formation of the assemblage.

Finally, cut-marks bear witness to hominid involvement with the fauna. A lateral fragment of a left radius showed traces which most plausibly result from disarticulation. A complete left phalanx 2 of a cervid was cut-marked proximally on its lateral face, also pointing to disarticulation of the bone. Moreover, cut-marks were observed on the cranial/ventral rim of an epistropheus (2nd cervical vertebra) from an animal of size/weight class 3 (Figure 3). Additional cut-marks were observed on a shaft fragment from the proximal region of a femur of an animal of size/weight class 3. Cut-marks indicate the disarticulation of skeletal elements as well as defleshing of carcass parts. Unambiguous traces of hominid marrow processing have not been observed.

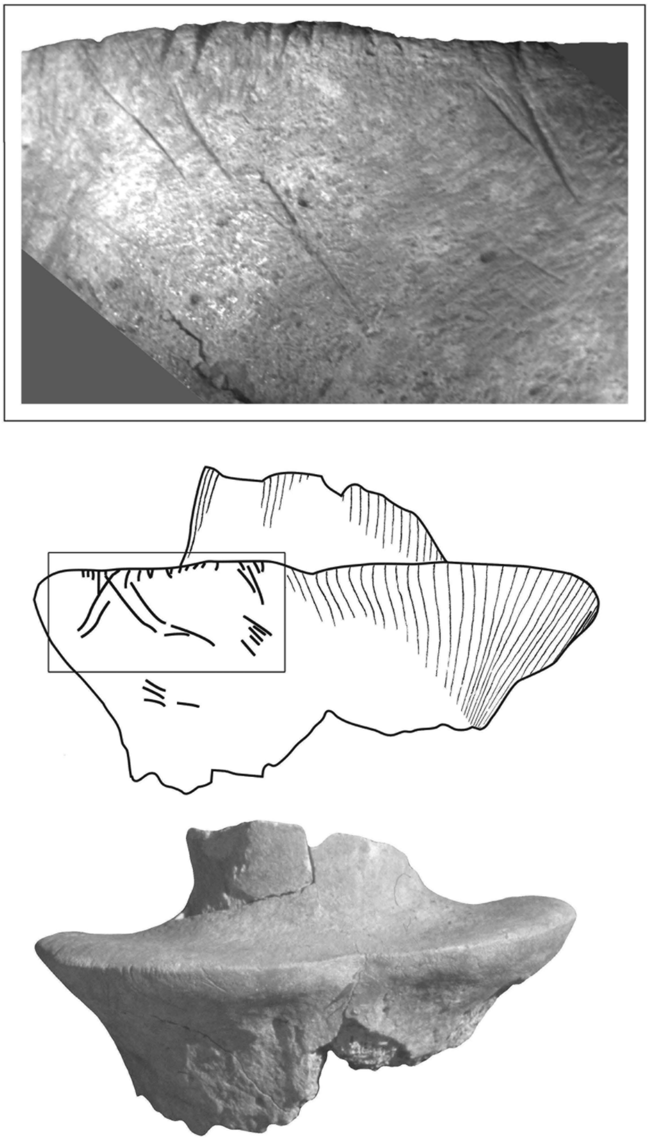


Figure 3. ‘Ubeidiya layer II-24, fragment of 2nd cervical vertebra of size/weight class 3 animal with cut-marks on cranial/ventral rim (cut-marks shown at 3x magnification).

Summary and discussion

The taxonomic composition of the layer II-24 assemblage is striking in the abundance of carnivore taxa (N=7). Cervidae and horses represent the most common elements within the fauna.

Skeletal element representation is similar for all size/weight classes, showing a dominance of trunk elements and often elements of the hind leg as well. Skeletal element representation does not correlate with either bone volume or bone shape, though it does correlate with structural density. Diagenetic bone destruction as well as carnivore activity are factors that might lead to density-dependent bone attrition. There is no indication that skeletal elements were selectively added to, or deleted from, the assemblage by hydraulic transport.

Longbone shaft fragments with rectangular fractures occur within the death assemblage. These fractures usually result from sediment compression after burial, thereby suggesting that most bones were complete at the time of burial. Differences in bone surface preservation, showing that the remains underwent differing diagenetic histories, were observed.

The death assemblage was affected by both carnivores and hominids. Several arguments point to the substantial role of carnivores in assemblage formation. Bone accumulations generated by hyenas are typically characterized by a large number of carnivore taxa and represent at least 20% of the total carnivore plus ungulate MNI (Cruz-Uribe 1991:475). For the layer II-24 assemblage, carnivores comprise 25.7% of the total MNI. Moreover, within hyena-generated accumulations, underrepresentation of epiphyses compared to shaft fragments is evident (Blumenschine 1988; Cruz-Uribe 1991). Dominance of shaft fragments as opposed to epiphyses is evident especially for bones in size/weight class 2. A further characteristic of hyena-accumulated faunas is the under-representation of small, compact bones, such as carpals and tarsals, which are entirely consumed by hyenas (Cruz-Uribe 1991). Though bone preservation as well as excavation techniques should have allowed recovery of these skeletal elements, they are nonetheless underrepresented within the layer II-24 assemblage. Apart from this indirect evidence, the presence of typical breakage patterns such as bone cylinders, as well as gnawing marks and the presence of coprolites, point directly to carnivore interference with the death assemblage. It seems highly plausible that the conically induced impact fractures observed in layer II-24 were also the product of carnivores. Micro-striations which may accompany hominid-induced impact fractures (Blumenschine & Selvaggio 1991) were not observed, and the grouping of these traces next to, or opposed to, each other on the longbone fragments points instead to carnivore modification.

Carnivores, therefore, were most probably a major agent in the layer II-24 bone accumulation. At least part of the fauna embedded in this layer might plausibly derive from a hyena den. In addition, the presence of natural background faunal elements cannot be excluded. The fact that the state of bone preservation varies considerably within the assemblage, as well as the suggestion, based on the fracture analysis, that a large number of the bones might have been complete when buried, together indicate that layer II-24 represents a palimpsest.

The presence of numerous stone artifacts, as well as the *in situ* preservation of the archaeological record, with artifacts and bones deposited together, indicate that hominids were also a major agent in the formation of the assemblage. This is underscored by the presence of cut-marks on bones resulting from disarticulation of skeletal elements. However, indications for marrow processing by hominids are not present. This particular characteristic is shared by the other 16 analyzed assemblages from the 'Ubeidiya Formation (see Table 1).

Assuming that cut-marked bones were present among the carnivore-accumulated part of the palimpsest, it seems plausible to suggest that hominid modification occurred before the bones were recycled by hyenas. If so, we are dealing with either remains scavenged from predator kills (the predators perhaps chased off by hominids before consumption), or leftovers from hominid hunting activities, or a combination of the two.

If we take a closer look at studies concerned with Plio-Pleistocene hominid scavenging opportunities, further conclusions can be drawn. These studies indicate that Plio-Pleistocene African hominids obtained their meat by scavenging small to medium-sized carcasses at natural death sites and felid kills. The latter strategy provides a significant amount of meat only if scavenging is confrontational, which some consider too risky (e.g., Dominguez-Rodrigo 2002). Only longbone marrow and the animal's brain are *regularly* available after felids have consumed their prey (Blumenschine 1986; Bunn & Ezzo 1993; Capaldo & Peters 1995). Viewed against this background, the scavenging hypothesis makes sense only if a bone assemblage yields clear evidence for marrow processing by hominids.

The apparent scarcity or absence (see Table 1) of traces of bone marrow breakage at 'Ubeidiya is of particular interest, as it is in marked contrast to the scavenging-based marrow-focused subsistence proposed by some researchers for early African hominids (e.g., Blumenschine

1995; Capaldo 1997). Either bone marrow processing remains invisible at 'Ubeidiya, or it was rarely practiced, or it was not among the subsistence strategies used by these Levantine hominids.

The absence of evidence for marrow processing could be due to its performance at locales different from the one represented at 'Ubeidiya. The density-mediated skeletal element representation documented for layer II-24, a characteristic shared by almost all of the faunal assemblages analyzed at 'Ubeidiya, prevents testing of this hypothesis.

Absence of marrow processing could equally indicate occupation of the sites of the 'Ubeidiya Formation only during particular seasons. As pointed out by Speth (1987), seasonal changes might have led to periods of resource stress for early African hominids to which they might have responded by preferentially targeting fat rather than meat, avoidance of high intakes of lean meat, and a focus on plant resources. Refraining from bone marrow exploitation, then, could indicate that the animals represented in layer II-24 were severely fat-depleted or that hominids had sufficient alternative sources of non-protein calories at that time of year. This scenario seems very unlikely for layer II-24.

An alternative explanation for the absence of indications for marrow processing is that *other sources such as meat provided for the necessary fat intake*. Assuming that scavenging opportunities were comparable for both African and Levantine Plio-Pleistocene hominids, considerable amounts of meat can be obtained regularly only by large-mammal hunting. If we further assume that animals whose bones have been found cut-marked at 'Ubeidiya were among the hominid prey, we have to assume that large-mammal hunting of animals of size/weight classes 2 and 3 was among the subsistence strategies of Levantine Plio-Pleistocene hominids.

We will have to await results of further taphonomic analyses from other Plio-Pleistocene Eurasian sites, such as Dmanisi in Georgia, to see whether the latter hypothesis can be substantiated.

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References

Bar-Yosef, O. & Goren-Inbar, N. (1993). *The Lithic Assemblages of 'Ubeidiya: A Lower Palaeolithic Site in the Jordan Valley*. Jerusalem: Qedem **34**.

Bar-Yosef, O. & Tchernov, E. (1972). *On the Palaeo-ecological History of the Site of 'Ubeidiya*. Jerusalem: The Israel Academy of Sciences and Humanities.

Behrensmeyer, A. K. (1975). The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology* **146**, 473–578.

Behrensmeyer, A. K. (1978). Taphonomic and ecologic information from bone weathering. *Paleobiology* **4**, 150–162.

Blumenschine, R. J. (1986). *Early Hominid Scavenging Opportunities*. BAR International Series S283. Oxford: British Archaeology Reports.

Blumenschine, R. J. (1995). Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at bones at FLK *Zinjanthropus*, Olduvai Gorge, Tanzania. *Journal of Human Evolution* **29**, 21–51.

Blumenschine, R. J. & Selvaggio, M. M. (1991). On the marks of marrow bone processing by hammerstones and hyenas: Their anatomical patterning and archaeological implications. In (J. D. Clark, Ed.) *Cultural Beginnings*. Bonn: Habelt Verlag, pp. 17–32.

Bocherens, H., Billiou, D., Mariotti, A., Patou-Mathis, M., Otte, M., Bonkean, D. & Toussaint, M. (1999). Palaeoenvironmental and palaeodietary implications of isotopic biochemistry of Last Interglacial Neanderthal and mammal bones in Scladina Cave (Belgium). *Journal of Archaeological Science* **26**, 599–607.

Bunn, H. (1997). The bone assemblages from the excavated sites. In (G. Ll. Isaac & B. Isaac, Eds.) *Koobi Fora Research Project. Vol. 5. Plio-Pleistocene Archaeology*. Oxford: Clarendon Press, pp. 402–458.

Bunn, H. T. & Ezzo, J. A. (1993). Hunting and scavenging by Plio/Pleistocene hominids: Nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science* **20**, 365–398.

Capaldo, S. D. & Peters, C. R. (1995). Skeletal inventories from wildebeest drownings at lakes Masek and Ndutu in the Serengeti ecosystem of Tanzania. *Journal of Archaeological Science* **22**, 385–408.

Capaldo, S. D. (1997). Experimental determinations of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *Journal of Human Evolution* **33**, 555–597.

Cruz-Uribe, K. (1991). Distinguishing hyena from hominid bone accumulations. *Journal of Field Archaeology* **18**, 467–486.

Dominguez-Rodrigo, A. (2002). Hunting and scavenging by early humans: The state of the debate. *Journal of World Prehistory* **16**, 1–54.

Frostick, L. & Ried, I. (1983). Taphonomic significance of sub-aerial transport of vertebrate fossils on steep semi-arid slopes. *Lethaia* **16**, 157–164.

Gaudzinski, S. (1996). On bovid assemblages and their consequences for the knowledge of subsistence patterns in the Middle Palaeolithic. *Proceedings of the Prehistoric Society* **62**, 19–39.

Gaudzinski, S. (n.d.). *Subsistenzstrategien Frühpleistozäner Hominiden in Eurasien*. Bonn: Habelt Verlag (in press).

Guérin, C., Eisenmann, V. & Faure, M. (1993). Les grands mammifères du gisement Pléistocène moyen de Latamne (Vallée de l'Oronto, Syrie). In (P. Sanlaville, J. Besançon, L. Copeland & S. Muhesen, Eds.) *Le Paléolithique de la Vallée Moyenne de l'Oronte (Syrie).* BAR International Series S587. Oxford: British Archaeology Reports, pp. 169–178.

Guérin, C., Bar-Yosef, O., Debard, E., Faure, M., Shea, J. & Tchernov, E. (1996). Mission archéologique et paléontologique dans le Pléistocène ancien d'Oubédiyeh (Israel): Résultats 1992–1994. *C.R. Acad. Sci. Paris* **322**, 709–712.

Lupo, K. D. (1998). Experimentally derived extraction rates for marrow: Implications for body part exploitation strategies of Plio-Pleistocene hominid scavengers. *Journal of Archaeological Science* **25**, 657–675.

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge: Cambridge University Press.

Marean C. W., Spencer, L. M., Blumenschine, R. J. & Capaldo, S. D. (1992). Captive hyena bone choice and destruction, the schlepp effect, and Olduvai archaeofaunas. *Journal of Archaeological Science* **19**, 101–121.

Martinez-Navarro, B. (1999). *Study of Lower Pleistocene Large Mammals from 'Ubeidiya: Comparisons with Eastern and Western Europe*. Unpublished Research Report to the Irene Levi-Sala CARE Archaeological Foundation.

Martinez-Navarro, B. (2000). *Study of the Lower Pleistocene Large Mammals from Israel: 'Ubeidiya and Gesher Benot Ya'aqov*. Unpublished Research Report to the Irene Levi-Sala CARE Archaeological Foundation.

Pfeiffer, T. (1999). *Die Stellung von Dama (Cervidae, Mammalia) im System Plesiometacarpaler Hirsche des Pleistozäns*. Frankfurt a. M.: Cour. Forsch.-Inst. Senckenberg **21**.

Picard, L. & Baida, U. (1966). *Geological Report on the Lower Pleistocene of the 'Ubeidiya Excavations*. Jerusalem: Israel Academy of Sciences and Humanities.

Potts, R. (1988). *Early Hominid Activities at Olduvai*. New York: Aldine de Gruyter.

Richards, M. P., Pettitt, P. B., Trinkaus, E., Smith, F. H., Paunovic, M. & Karavanic, I. (2000). Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proceedings of the National Academy of Sciences USA* **97**, 7663–7666.

Roebroeks, W. (2001). Hominid behaviour and the first occupation of Europe. *Journal of Human Evolution* **41**, 437–461.

Shea, J. (1997). Neandertal and early modern human behavioral variability. *Current Anthropology* **39**, 45–78.

Speth, J. D. (1987). Early hominid subsistence strategies in seasonal habitats. *Journal of Archaeological Science* **14**, 13–29.

Stekelis, M. (1966). *Archaeological Excavations at ʻUbeidiya, 1960–1963*. Jerusalem: Israel Academy of Sciences and Humanities.

Stekelis, M., Bar-Yosef, O. & Schick, T. (1969). *Archaeological excavations at ʻUbeidiya 1964–1966*. Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (1973). *On the Pleistocene Molluscs of the Jordan Valley*. Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (1980). *The Pleistocene Birds of ʻUbeidiya, Jordan Valley.* Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (Ed.) (1986). *Les Mammifères du Pléistocène Inférieur de la Vallée du Jourdain à Oubeidiyeh.* Paris: Association Paléorient.

Tchernov, E. (1987). The age of the ʻUbeidiya Formation, an Early Pleistocene hominid site in the Jordan Valley, Israel. *Israel Journal of Earth Sciences* **36**, 3–30.

Thieme, H. (1997). Lower Palaeolithic hunting spears from Schöningen, Germany. *Nature* **358**, 807–810.

Chapter VII

Bands and Other Corporate Hominid Groups in Acheulian Culture

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Abstract

This chapter offers the thoughts of a social anthropologist on the social life of the Acheulians, in the hope that it will renew some old discussions and lead on to new ideas. As there is little direct evidence about Acheulian society, I shall work, with the necessary caution, from our quite detailed knowledge of contemporary hunter-gatherers. My argument, in a nutshell, is that one-to-one (*dyadic*) personal relationships and task-oriented egalitarian (*corporate*) groups were the foremost forms of collaboration among Acheulians. They established numerous dyadic relationships for various short-term or long-term joint activities, such as companionship, sexual relations, and reproduction. They also participated in numerous corporate groups, for such tasks as food-gathering, hunting, and the manufacture of utensils. The most inclusive corporate group was probably the band, which provided its members with physical and social security and exerted moral control. It was also a very important location for convivial play, talk, dancing, and feasting (*sociability*), which fostered trust among members. It is very unlikely, however, that the Acheulians had either long-lasting domestic groups (or families), kinship ties extending beyond the links between mother and child and between siblings, or territorial organizations, such as the tribe.

Introduction

I proceed in the following manner. First, I address the methodological problem of how ethnographic data from contemporary societies may become useful for the study of the Acheulians. Second, I examine the concept of the corporate group which, I believe, may help in understanding Acheulian society. I use the well-studied corporate descent groups as the paradigm for other corporate groups, making the necessary allowances and corrections. Third, I discuss the various dyadic relationships and corporate groups that presumably existed in Acheulian society, paying special attention to the social structure of the band. Finally, I explore some implications of life in bands with regard to social control, territoriality, and migration.

The methodological problem

I follow the historian Marc Bloch in arguing that it makes sense to understand the past by the present, because “the natural progression of all research is from the best (or least badly) understood to the most obscure” (Bloch 1953:45). Still, the difference between our times and the Acheulian period is so immense, and our capacity to break with deeply engrained habits of thought so limited, that this exercise alone is not sufficient. What is really needed is a special methodology that allows us to apply contemporary ethnographies to Acheulian conditions. In principle, every anthropological study should develop a methodology that precisely fits the theoretical problem discussed and the people studied (not that we always meet that requirement). I argue that the “social field” approach, first proposed by psychologist Kurt Lewin (1951) and further developed by the Manchester school of anthropology (Van Velsen 1967) can be of some help, provided we turn it on its head. When studying a social field, we concentrate our attention on a small social aggregate, either an individual or a number of linked persons, and examine all the environmental factors, whether "natural" or social, with which it interacts directly. This procedure allows us to produce full contextual studies of social aggregates. It works with a totally open system that respects neither conceptual nor territorial boundaries. It examines the impact of such factors as colonial administrative practices, the terms of trade for local products, the laws regulating land tenure, and the availability of roads and other technological infrastructures on the social aggregate studied (see Marx 1980:19–21).

When the study has reached that stage, we turn the social field approach upside down, for now, momentarily, our aim is not so much to understand the social aggregate studied as to identify the factors impinging on it and assess their impact. Our main concern henceforth will be to eliminate or neutralize these factors, and to imagine how people would have behaved in their absence. Thus, a study of a contemporary band, say of the well-studied Bushmen or San, may portray people living in domestic groups and bands, owning property such as trees, led by chiefs, and laying claim to a territory. Once we realize that many of these people are migrant laborers on farming estates and mines, that they exchange their labor and the products of their region for manufactured goods and foodstuffs, and that they are encapsulated in states and surrounded by other peoples who press on their territories (Woodburn 2001:10), certain aspects of their society can be understood as adaptations to these environmental forces (/Useb 2001 criticizes anthropologists for not doing enough of that when discussing theoretical issues, such as leadership among Bushmen). Furthermore, one may find that these forces affect some members of the band more than others, and learn a great deal from such internal co-variation. The next step is to imagine what these band societies would be like if their members did not work for wages, engaged only in limited barter trade, and were not hemmed in by states and other claimants to the land. Then one may realize, for instance, that only when children can work for their parents and can provide them with security in sickness and old age do they become valuable assets and give purpose to the establishment of a domestic group. Or one may discover that only exchange value determines whether an item is deemed worth owning, that institutionalized chiefship is found only in state societies, and that territoriality exists only where land is scarce and its free use contested. The conclusions of such reflection can then be cautiously applied to Acheulian conditions (a good example of such a reconstruction, though of a relatively recent past, is Colchester 1984).

In addition to the many social forces affecting ancient hunter-gatherers, there were environmental conditions to which they had to adapt, such as long-term, short-term, and seasonal variations in climate, the changing features and morphology of the landscape, the availability of food, water, fuel, shelter, and lithic material in various locations, and competition with sometimes more efficient and dangerous predators (such as lions) and more agile gatherers (such as birds). We must also consider early man's limited capacity to cope with illness and accidents, and the difficulty of raising enough children to replace the elder generation and maintain bands large enough to ensure survival. When we reflect on the exigencies and risks affecting the lives of Acheulians, it dawns on us that the mere survival of man must often have hung in the balance.

A survey of the vast literature on contemporary foragers and hunter-gatherers provided much useful material for a reconstruction of Acheulian culture. However, the most relevant data came from studies of the pygmies in Congo's Ituri forest. These people often live in the villages of Bantu farmers, but also spend many months on end in the forest. The sojourn in the forest may last up to six months, during which their contacts with the outer world are almost suspended. Among the numerous studies of pygmies I found Turnbull's *The Forest People* (1961) most useful. It is a very intimate, sensitive, and emphatic ethnographic account of the life of one band in the Ituri forest. The very detailed and sophisticated studies of Bushmen (or San) of the Kalahari desert by Lee (1984) and his associates, and by many other scholars, were also very helpful, although their accounts do not always spell out the implications of the Bushmen's heavy dependence on their Bantu "masters."

Although we possess a great deal of information on contemporary hunter-gatherers, we cannot fully explain the variability in their social behavior, as Kent (1996:12–14) has pointed out. How much harder is it to fathom the social practices of Acheulians, about whom we know so little? The widely accepted premise that their behavior was uniform and changed little for more than a million years only makes matters worse. For it denies a major aspect of their humanity, namely their capacity to learn, and thus makes it impossible for us to imagine their behavior. We must also admit that anthropological theory has, right from the beginnings (Morgan 1974; Boas 1966), put an ideal western-type family at the center of "social organization" and derived kinship, descent, and the tribe from it. More than a hundred years later, and in spite of David Schneider's groundbreaking study of *American Kinship* (1968), the anthropologist's view of kinship is still almost identical with that of the founding fathers of anthropology and, more curiously, with that of the American man on the street. While Morgan and Engels postulated a state of primitive promiscuity between early men and women, neither they nor any other anthropologist ever described a society that even approximated such conditions. In order to overcome this bias, I suggest that another social form, namely the corporate group, was not only the earliest form of collaboration among hominids, but also preceded the family and its presumed derivative groups.

What are corporate groups?

Corporateness is the matrix of political groups, from the smallest to the largest. I define the corporate group as a number of persons collaborating as equals on a specific task (Marx n.d.). Many of today's anthropologists would subscribe to this definition. Its advantage lies in that it encompasses all the forms, sizes, and varieties of long-term and short-term corporate collaboration, such as bands, work groups, and voluntary associations. Earlier anthropologists, however, used a definition that put the emphasis on the continued existence of the corporate group, as an organization that could outlive its original members. They employed the concept mainly in the discussion of corporate descent groups and, furthermore, gave these groups undue weight in the analysis of "social structure," although they went into action only intermittently. They did not pay sufficient attention to the many other corporate activities that fill the daily life of people. I examine these corporate groups in greater detail. One of the most common corporate groups is the band, which I discuss at some length. I deal only briefly with dyadic relations, mainly in order to dispel the idea that they necessarily combine into connected social networks, such as those of kin.

It is often taken for granted that the corporate descent group is the prototype of the small political group. In reality, every "tribal" society is made up of many types of task-oriented corporate groups, in addition to the corporate descent groups. Some simple societies (for instance, most Bushman groups) may lack descent groups altogether, while the descent groups in some other societies are not corporate. The Bedouin of South Sinai, for instance, have non-corporate descent groups, which serve only as an imagined link between the individual and the tribe. But these Bedouin participate in numerous corporate activities, such as smuggling rings and tribal pilgrimages. Nor are corporate groups confined to simple societies. For many large modern organizations, such as armies, state bureaucracies, and business and industrial organizations, also comprise small corporate contingents. These groups of employees and retainers are always embedded in larger groups and may sometimes act in concert with them, but may as often pursue their own corporate agenda. Lastly, one should note that non-corporate groups may almost instantaneously become corporate, and that groups claiming to eschew politics may engage in political activity whenever it suits their interests. And any group, whatever its manifest purpose, will continually engage in internal jockeying for power and, should the occasion arise, transform itself into a group specializing in political activities. Such changes have been documented in domestic groups, residential groups, factions (groups focused on leaders), occupational associations, and religious sects.

We possess numerous studies of the politics of corporate descent groups in Middle Eastern societies (see Eickelman 1989:75–76 for references). But these studies do not exhaust the repertoire of corporate groups. For instance, family trucking cooperatives in Syria (Rugh 1997:84), the pastoral enterprises of extended families among Israeli Bedouin (Abu-Rabia 1994, Chapters 2 and 3) and Egyptian Bedouin (Hüsken and Roenpage 1998:52–54), and the saving associations of urban women in Cairo (Early 1993:5) are often corporate. Each of these groups may also become politically active.

I first look at corporate descent groups in the Middle East and, where necessary, also refer to the classical studies of African tribal societies. I examine the ideological foundations of these groups and enquire how members are recruited, how the groups operate, and for what purpose. In the Arab world the corporate descent group goes under various names, such as *hamula*, *khams*, *qom*, *batn*, and *fakhdh*, and in daily conversation people also nonchalantly use terms that properly should denote the family (*ahl*), extended family (*'a'ila*), and tribe (*qabila*). This multiplicity of terms is not as imprecise as it may appear, as people think of these groups as evolving self-transforming entities. Most anthropologists would go along with the following working definition: the corporate descent group is an egalitarian group of adult men who claim descent from one (male or female) ancestor; its task is to assist any member or members who have been physically attacked or whose property rights (mostly in land) have been infringed on by members of another descent group (for various definitions and further references, see Fried 1957:23; Befu & Plotnicov 1962:64; Buchler & Selby 1968:70; Hayden & Cannon 1982:133–135). The six chief characteristics of the group are, according to the definition, that it is composed of men only, that members are recruited by descent, that it is an egalitarian group, that it functions in defense of persons and property, that it is activated when attacked by outsiders, and that it may exist in perpetuity. This definition needs corrections, especially if it is to apply to all corporate groups.

Corporate descent groups recruit men only, because they are trained to fight, whereas women are not allowed to acquire martial skills. But in the absence of men, women may take their place in battle. Thus, Beck reports that the women of the Qermezi, a Qashqa'i descent group, rushed to defend their farmland against peasant invaders: "At the height of the conflict, 13 Qermezi men and 30 women faced 150 peasants and their supporters. Both sides, including women, sustained injuries" (Beck 1991:95). Corporate groups that regularly engage in other activities include both men and women. For instance, among some Bedouin pastoralists all the members of a household, men, women, and children, jointly own and care for the flock. In this context they act corporately (Abu-Rabia 1994, Chapters 2 and 3).

Members are formally recruited by descent from a distant ancestor. They can usually enumerate ancestors that go back two or three generations, but will admit that they do not remember the full details of their connection to the ancestor. There is always a gap in their genealogical knowledge, separating the apical ancestor from the living descendents (Peters 1990:99). Even when the genealogy shows that the ancestor is only five generations removed from the living members, they will admit that they do not remember the names of his or her direct descendents and that in all probability the ancestor is much further removed, "many more than five generations" (Marx 1967:188). Because of this structural genealogical amnesia, all of the members are equidistant from the ancestor, who thus becomes a figurehead symbolizing the boundedness of the group, its unity, and the formal equality of its members. The implication is that while many members are connected by kinship ties, their obligations as kin are kept at bay, as they may clash with the group's functioning.

Furthermore, membership is not necessarily determined by descent. True, a man becomes a member by birth. But this does not mean that he will always take up the membership or remain a member all his life. As an adult he can choose not to join the group. All he has to do is to move to another location, or to join another group. He can indicate to fellow members at any time that he wishes to leave the group, simply by not fulfilling his contractual obligations. The group can also decide to expel a troublesome member, for instance a man who has had too many violent encounters (Marx 1967:199–200, 239–241; see also Moore 1978:122–124). The group may also extend membership to strangers or merge with another descent group. We must therefore conclude that, in practice, membership of the group is almost voluntary, and even persons born into the group choose if and when to join and when to leave. What unites the group is the joint purpose, while descent is only a boundary-setting rule. Every corporate group has a rule determining who is a member and who is not. Thus membership in bands is conferred by residence in the camp; in hunting groups, by participating in the hunt, and so forth.

Another characteristic of the corporate group is that all members share the same rights and obligations (Fortes 1970:306). It cannot be otherwise; for if members are expected to risk their lives for their fellows, they must be sure that this is done on a reciprocal basis. Many groups take active steps to ensure the commitment of members, especially of the younger men who do most of the fighting. Thus, when a Negev Bedouin marries, the group encourages his parents to give him a proportional share in the family's farmland and herds, "as custom demands." By doing so they not only give away part of the household's productive resources, but also tend to lose the son's labor. As this clearly goes against the parents' interests, they delay the transaction as long as possible. But the other members of the corporate descent group wish to turn the young men into property-owners, and thus make them equals of their property-owning fathers. For this will induce them to risk life and limb, in order to protect both their own and the group's interests. While life inheritance appears to enhance equality between members of the group, it also exposes the fact that there still is some differentiation between the elders who make the policy decisions and fight in the second rank, and the younger men who bear the brunt of the fighting (Marx 1987:169–171).

The principle of formal equality is preserved in all corporate groups, at least on the declarative level. In Bedouin society, for instance, each member has the same right to be protected, just as in Western states every citizen participates in elections on the basis of one person, one vote. In practice, numerous factors differentiate the members, for instance ranking and stratification (Fried 1957:23–24) or leadership. Max Weber (1947:133) has shown that there can be no corporation without a leader or leaders. But I should add that in bands, for instance, leadership may be quite informal and may not be vested in one person. A person may simply assume leadership whenever the situation requires it. There are also individual differences between wealthy and poor members, between clever men who persuade their fellows to support them even in doubtful cases and simple men who are bound by the formal rules, between men who can count on the individual and corporate support of family members, friends, neighbors, and other corporations, and others who stand alone. My main point is that a corporate group cannot operate without these internal differences in status and power and the subdivision into sections and cliques of unequal power. These divisions articulate the group, facilitate communication between members, and thus permit the group to mobilize quickly.

Formally, the descent group serves only one purpose, namely to protect the lives, land, and property of its members. In practice, it behaves very much like other interest groups, that are set up for a specific purpose, but may quite easily shift and change their concerns. They may at any suitable moment transform themselves into purely political groups. It should not come as a surprise to learn that Negev Bedouin who moved into new towns and lost all their land and flocks retained their corporate descent groups. In the towns the descent groups represented their members in local political arenas and engaged in political resistance to the State's land policies (Jakubowska 1992). A group that has been set up to perform a particular task may then quite easily and rapidly assume other duties and still remain corporate.

The group responds to external stimuli and thus acts only intermittently. In between actions it exists mostly in the minds of its members. Of course, they do receive daily reminders of their obligations as members, for instance by staying in a camp with some other members of the corporate group, so that whenever they attend at the guest-tent and drink coffee together they represent the group. Similarly, when interlocutors require them to state a "family" name, they usually give the name of the group's eponym. In most other corporate groups, people do not need reminders that they are members, for they usually get together for a particular task, often a regularly recurring one. Once the task is accomplished the group can disperse, and on the next occasion reassemble, perhaps with a changed membership.

It is a peculiarity of corporate descent groups that members are activated by a symbolic cue. The news that someone has injured the economic interests of members is not sufficient ground for mobilization. They must also be informed that the blood of a member has been shed. Then they put aside whatever they are doing at the moment and rush to the site of the fighting. The member is therefore called a "protector of blood" (*dammawi*), for common blood is the ideology that underlies the group's unity. The members believe that as descendents of one ancestor they share the same blood and are bound to defend the blood of their fellows. As there must be bloodshed before the group can be mobilized, blood is drawn in every fight. Eventually it may emerge that the victim sustained only an imperceptible scratch. An astute leader can, therefore, easily simulate a bloody clash and draw members into ill-considered disputes, including ones that are quite outside the group's best interests.

Corporate groups are in constant flux and some groups may be quite short-lived. A group that has grown too large tends to split up; one that is too small may disband or join another group; groups are racked by internal squabbles and may split; members who feel that the group has deserted them may secede and establish new groups. In the wake of such splits the eponyms of the corporate descent groups will also be realigned.

Joint property is not a necessary prerequisite of a corporate group. One often encounters corporate groups that do not hold property in common. Among the Negev Bedouin, for instance, farmland is owned individually, and pastures by tribal federations. But that has never prevented corporate descent groups from protecting private or communal property. Even where there are customary methods for redistributing joint property, such as the periodic reallocation of common land (*musha'*) in some traditional Middle Eastern villages (Aswad 1971:43–44; Gerber 1993), corporate descent groups effectively protect their members' interests.

Is the belief in the corporate group's perpetuity then no more than a legal fiction that disguises its fickle and changeable nature? Part of the answer is that the underlying joint interest brings the members together. But there is more to it, for members continue to collaborate even when their interests diverge. Their collaboration grows chiefly out of living together and participating in what Simmel calls "sociability," activities designed to engender trust and closeness between people. Sociability takes place in social gatherings, "in which one 'does as if' all were equal, and at the same time, as if one honored each of them in particular" (Simmel 1964:49). Participants in these gatherings play games and entertain one another with stories, jokes, and good-natured banter and gossip, all within limits prescribed by tact and politeness. Sociability is a necessary human activity in which "the great, perhaps the greatest, problem of society finds … a solution which is possible nowhere else. This problem is the question concerning the proportions of significance and weight that, in the total life of the individual, are properly his, and properly those of his social sphere..." (Simmel 1964:45; Dunbar 1996 attributes a similar function to mutual grooming among nonhuman primates and to gossip among humans).

Where the corporate descent group is the paradigmatic corporation, other corporate groups are cast in its image. Thus, Eickelman (1989:156) reports that, in the urban Moroccan neighborhood he studied, "participation in factional alliances, ties of patronage and clientship, and common bonds developed through neighborliness" are all viewed as corporate. These groups enlist members according to their interests. But both members and outsiders may describe them as joint descent groups, so as to fit them into the widely accepted folk model of a society made up of a series of ever more encompassing descent groups. Their association is often described as based on common blood, especially when the group defends the members' bodily safety.

Recent studies of complex "tribal" politics (for instance, Kressel 1996) have shown that political activities are performed by a variety of corporate groups and individuals and not necessarily by descent groups. But the anthropological community has not immediately responded to such arguments. Only when it adopts the premise that social life is made up of many different organized activities, each as important as the next, will it be able to appreciate the importance of corporate groups. Then it will realize that corporate groups carry out many, if not most, of the activities of daily life.

The gist of the argument so far has been that corporate groups are flexible egalitarian interest groups, which may undergo a variety of rapid transformations. They are sometimes enduring, but are more often short-lived. Membership is almost voluntary, and is not confined to a particular category of persons, such as the direct descendents of an ancestor. There is considerable movement of individuals in and out of groups. The groups are internally segmented; there are leaders, cliques, and status differences, and competition for status and resources. These internal divisions and day-to-day interactions allow the group to mobilize when required. In all of these respects corporate groups resemble other types of groups, such as domestic groups, voluntary associations, and business partnerships. Conversely, I argue that any non-corporate group may on occasion become corporate and engage in manifestly political activities. I argue furthermore that corporate groups continuously change their structure and practices in the course of interacting with other groups. The image of an amoeba that constantly changes shapes, fuses into another amoeba, or splits in two may fit them well. It may thus be quite misleading to classify a group as a corporate descent group, faction, etc., without inserting an immediate temporal and situational qualifier.

I must still explain the argument that dyadic relationships, and especially kinship links, do not necessarily build up into groups or close-knit social networks. During fieldwork in the Negev my Bedouin friends worked hard to explain to me that the corporate descent group (*khams*) dealt only with the defense of members, and was not a group of kinsmen. They also argued that kinsmen did not link up in a group or network. While they recognized numerous categories of male and female relatives, they thought about each of them as a potential partner in a useful dyadic relationship and about some of them as totally reliable supporters. Thus, a mother's brother was someone who could be fully relied upon, more even than a father or brother, to help his sister's son in any contingency. They also maintained close ties with one or more brothers and sisters, but kept their distance from the others. Yet when any sibling, whether close or distant, made a demand of any kind, they did not refuse him or her. The Bedouin felt that their connections with these persons were the outcome of sharing, or having recently shared, the same domestic environment. They never thought that all of these relatives were part of an ego-centered network. Nor did they conceive of kinship as a way of ordering relationships, or as the organizing principle of groups. I follow their lead because it fits in with practical experience, not only among Bedouin but also in other social environments. When we apply this insight to the Acheulians, we can assume that they established enduring dyadic ties with a very small number of relatives. The closest ties must have been those between mother and child and between siblings of both sexes, but not necessarily between biological fathers (genitors) and their children.

Corporate groups in Acheulian culture

Is this analysis pertinent to the understanding of Acheulian culture? It is, on two counts. First, it adds some new sociological ideas to the study of ancient man. Paleoanthropology has hitherto deeply engaged a wide range of disciplines, such as anatomy, geology, botany, primate studies, and genetics, and also made some use of the ideas and information accumulated in social anthropological studies of contemporary humans. Indeed, the ethnography of hunter-gatherers has interested prehistorians for a long time, perhaps beginning with Sollas (1911) and right into the present. But they concentrated more on the daily life of the individual than on the corporate groups, including the bands. Second, it tries to give the concept of "culture" a wider meaning than that of being a style of tool production, and seeks to learn more about the social behavior of the people who made the tools. Some prehistorians (for instance, Isaac 1986:234; Wynn 1995) have explored a very rewarding avenue toward understanding the Acheulians: they realized that the production of stone tools required great intellectual capacity. As Klein puts it, "the wonderful three-dimensional symmetry of many late Acheulian hand axes may mark an … important [cognitive] advance that now allowed the people to rotate the final tool in their minds while it was still encased in the raw rock" (Klein with Edgar 2002:143). Madsen (2003) goes even further. He shows experimentally that Acheulians developed consummate manual skills. Not only could they visualize the form of a completed tool in the pebble they utilized, but they were also capable of planning the whole sequence of knapping, a process of sometimes more than a hundred consecutive and interrelated steps. Furthermore, he found that flint-knapping required many years of training. The knapper learned to distinguish between varieties of flint or basalt, to plan the knapping procedure according to the material and the desired product, and to deliver each stroke with the right amount of force at the precisely appropriate angle. With the combination of knowledge, skill, and imagination acquired in long years of training, he or she could produce a perfect cleaver or handaxe in half an hour of careful, intensive work. Thus, the manufacture of a handaxe was a task that exercised most of man's mental faculties. It equaled the complex qualities and training a modern sculptor needs in order to create a statue or, in a more prosaic vein, a dentist to fill in a cavity. The lithic products of the Acheulians thus allow us to contend that they applied the same intellectual qualities to their social behavior, irrespective of their smaller brains. (We should however bear in mind that the cranial capacity of Acheulians varied widely.) In this light we can examine the forces shaping their social life, or rather the dialectic interaction between the people and their environment.

I therefore assume, on the one hand, that the Acheulians engaged in a variety of dyadic relationships and participated in numerous corporate groups, including the band. On the other hand, it seems to me reasonable to argue that some of the basic components of contemporary "simple" societies, such as the domestic group, kinship networks, and the tribe as a territorial organization, did not exist. I should note that a minimal definition of territoriality, as a bundle of rights to a vaguely defined and undefended area, is in place here. The Acheulians may have claimed very modest rights, such as prior access to beehives and certain fruit trees in the vicinity of a camp, though nothing as elaborate as the complex rights of Bushmen to protect their territories against other Bushmen. Ironically, these rights were regularly overridden by Bantu herders (see Barnard 1992:233).

The domestic group (or family), as a union of at least one woman and one man for purposes of production and reproduction, could not have existed among the Acheulians. If one looks at reproduction as part of the productive process, it becomes clear that in their band societies only the existence of gathering and hunting groups could assure conditions for the survival of children. Furthermore, the band could support the adults if they became incapacitated or too weak to take care of themselves. The parents did not need children, and once the children were weaned they did not require parents. The domestic group can flourish only in a densely populated environment in which land and other goods become scarce resources. Children then become an important resource owned jointly or separately by parents. They are worth owning only when they can contribute labor exclusively to their parents or sustain their parents in old age. It is thus the joint ownership of children and other productive resources that encourages men and women to form relatively stable unions. This idea was broached by Morgan in 1877 (Morgan 1974:512), was elaborated by Engels (1972:128), and was again taken up by Meillassoux (1981:16). While "Stone Age" band societies were not exactly "the original affluent society" that Sahlins (1974:1) made them out to be, their members could be confident that the environment would satisfy their modest demands on a daily basis (Bird-David 1992:29); therefore, children were needed neither for work in a domestic group nor for the sustenance of the old and sickly. Bands usually had, and still have, access to sufficient quantities of food, such as fruit, nuts (as shown for Gesher Benot Ya'aqov by Goren-Inbar et al. 2002), vegetables, mushrooms, berries, insects, and tubers (Turnbull 1965:149). Preliminary results of studies of today's hunter-gatherers indicate that a man or a woman requires three to four hours a day (Lee 1968:37; Hawkes et al. 1997:556 calculated a figure of four to five hours) to collect enough food for him- or herself and a dependent. Where hunting and fishing is also practiced, temporary surpluses of food become available (Sahlins 1974:21–23). For instance, when the carcass of an elephant must be disposed of quickly (as at Gesher Benot Ya'aqov; see Goren-Inbar et al. 1994:109), many mouths – indeed, a whole band – can be fed. In these conditions people engage in "immediate-return" economies, in which "individuals and groups go out for part of most days to obtain their food and other requirements which are then consumed for the most part on that particular day or casually over the days that follow" (Woodburn 1980:98); therefore, only small amounts of food are prepared for storage, and all food is shared among the members of a band.

Where food and physical security are provided by the band and no property is accumulated, there is little point in establishing an enduring marital tie in order to "own" children. This accords, up to a point, with the argument proposed by Klein with regard to *Homo ergaster*. In a daring reduction from physiological form to social behavior, he argues that "the reduced size difference [of males and females] may signal the onset of a more typically human pattern in which male-male competition was reduced and male-female relationships were more lasting and mutually supportive" (Klein with Edgar 2002:101). One may subscribe to this statement on sociological grounds, but should add that while men and women did cooperate for longer or shorter periods in raising children, they did not expect to raise them to adulthood. Men and women were "mutually supportive" only as long as they stayed together, and the same was true for their relations with their offspring. A woman and a man could stay together for one or more child-raising sequences, and may thus have set up a relatively long-lasting corporate group. More often, however, "unions between men and women [were] fragile. After weaning, and sometimes before, children [were] adopted by members of the band as a whole" (Meillassoux 1981:16). Even among today's hunter-gatherers, encapsulated as they are in wider society, men often "desert" their wives and children in order to set up new short-lived unions (Blurton Jones et al. 1996:172–175). According to Turnbull (1965:274–275), the alliances of men and women among the Pygmies, which he nevertheless calls "marriages," are quite unstable: "A marriage is effected by living together; divorce is effected by one or other spouse simply going to live elsewhere." The "young married couples are held responsible for reproduction, but only to a limited extent for the rearing and education of their children, for beyond the age of three or four the child becomes the responsibility of the band as a whole" (Turnbull 1965:113). The children are from birth onward fondled and fed by all the members of the band. The parents' responsibilities are rapidly reduced, leaving both them and the children free to forge new alliances. Nor do the parents see it as their exclusive task to train the children. Any slightly older and more experienced member of the camp can instruct them in the few techniques that they do not pick up by imitating the adults. But they learn most of the life skills while playing. "From the time they can walk both girls and boys play 'house'," including foraging, hut construction techniques, and sexual behavior, reports Turnbull (1965:124). Among the Hadza too, "boys learn their bow-and-arrow hunting knowledge and techniques and their tracking skills mainly informally from other boys only a little older than themselves" (Woodburn 1980:107). The children, moreover, are eventually affected by the changing allegiances of the parents and, caught up in the dynamics of the band's changing membership, are likely to move elsewhere. Turnbull (1965:116) informs us that the children may "either be adopted by or simply live for a while with another family in the same band; or they may be adopted by a family in another band and go to live there, even if their parents continue living together in their home band".

Rearing children was just one of a variety of corporate associations between Acheulian men and women. There were probably other associations, for sexual gratification, food gathering, hunting, tool production, and feasting. Again, most of these would be short-term relationships, which could be extended to longer periods. Thus, Mbuti women never forage on their own but "only go off in twos or threes to gather" (Turnbull 1965:167); hunting groups comprising men, women, and children of "between six or seven and thirty nuclear families" go out almost daily (Turnbull 1965:154). Bushmen often establish unions for sexual pleasure and "live together for short periods without being married" (Thomas 1958:85). At Mbuti death festivals every household in the camp must contribute food and everyone must sing in order to ensure success, thus showing that the camp is corporate (Turnbull 1965:264).

If there was no domestic group, then kinship networks were out of the question. For kinship refers to the presumed continuity of the ties formed among the members of a domestic group as a consequence of living together for many years, a condition that prevails in stratified societies where households own productive resources, such as land, herds, and tools, and of course children. Where there was no lasting domestic group, there could be only very few remembered links between persons who were close to one another during the years in which they participated in reproduction: those between a woman and her sex partner or her child-raising partner, between a mother and her children, between siblings and, occasionally, between a biological father (*genitor)* and his offspring. He could hardly become a social father (*pater*) in Acheulian times.

The almost total absence of kinship in the more isolated band societies has been noted, and explained away, by ethnographers. When Turnbull studied the Mbuti Pygmies' personal terminology, he discovered that they classified persons only by relative age: they were either old people, members of ego's parents' generation, siblings, or children (1965:110). There simply were no kinship terms. He found it quite difficult to accept this, but in the end admitted that the terminology "clearly cut across all strictly kinship considerations. This can to some extent be construed as a denial of kinship ties" (1965:272). Silberbauer too begins by arguing that "kinship was ... important as an organizing principle for the ... G/wi" Bushmen [whom he calls Basarwa] of the Kalahari (Silberbauer 1996:55), but then finds that their kinship terminology "yielded a small number of distinctive categories, some of which were very broad in their scope" (1996:55–56). Kinship ties, in the sense used by anthropologists, are ego-centered and distinguish kin not only by their generational position, but also by their distance from ego's family of origin. Most of these distinctions are not developed in the isolated band societies, as the ties between persons are fleeting and changeable.

There certainly were no tribes or other territorial entities among Acheulians. Where there were no "others" to contest a band's rights in a particular territory, where free access to all land was a condition of survival, and where people moved easily from one group to another, strictly territorial groups were unlikely to develop. Nor were groups likely to unite in order to defend their rights to an area of land. So the band, a basically non-territorial mobile group with relatively fluid membership, was the largest social group. Bands are arguably the most complex kind of corporate group, and anthropologists have studied them very intensively. Like today's bands, the ancient band must have been corporate in sharing food, providing members with physical and social security, helping them in sickness and bereavement, and burying them when they died. The band would encompass other, more or less ephemeral, corporate groups, such as food-gathering groups, groups of hunters, and tool-making groups. Hunting groups may sometimes have been recruited from different bands (see Marshall 1976:357).

The members of a band tend to camp together. The camp would comprise a number of households, some of which might combine as a section of the band and set up a tight cluster of huts within the camp, and be crosscut by groups of age-mates (Turnbull 1965:112–116). Although a band moves in constant search of food, it will usually develop an attachment to a particular region. If the members are not persuaded by conflict, storm, fire, or the death of a member to migrate, they will stay in a campsite until the food supply in the vicinity is exhausted, and then move on to another site (Lee 1972). Thus, a Mbuti band of a dozen or so households moves camp every month (Turnbull 1965:221). Two separate surveys of Bushman bands report a band size of 18 to 48 individuals moving zero to seven times a year, and bands of 19 to 42 individuals moving four to eighteen times a year (Barnard 1992:226). A band may return to sites it visited earlier if the food supply has recovered. It may claim priority of access to a territory, but this would be far from constituting a kind of territoriality. For that would work against its interest, which is to seek food wherever it is available; therefore, it will allow others access to the land it occupies at the moment. It will have a limited territorial claim only to special localized concentrations of resources, such as perennial springs (Valla 2000:15; Barnard 1979:141) or clusters of fruit trees and beehives, often for only one season (Turnbull 1965:168; Schebesta 1928:279). Territoriality may develop only when the population is so dense that people must compete for land (Peterson 1979:121), a situation that was unlikely to arise in Acheulian times, when no settled populations encroached on the hunter-gatherers. For movement demands that people travel light, which is another reason why they raise few children (Kent 1996:146; though Blurton Jones et al. 1996:162–163 claim that contemporary hunter-gatherers "maximize the production of descendants"). And while holding on as long as possible to those too weak to keep up with the band, they abandon them in the end (Sahlins 1974:34). Thus, Turnbull speaks about a Pygmy who "had so many children that … he could not remember all their names... [He] was getting too old to follow the hunting band with ease, and he was afraid of being abandoned." To forestall such a possibility he moved close to a Bantu village (Turnbull 1961:36–37). Woodburn is more explicit: "Hadza abandon the seriously ill whether they are their close kin or not" (1980:105). And an old Bushman woman put it even more succinctly: "It is bad to die because when you die you are all alone" (Thomas 1958:123).

As the band moves, its membership changes quite rapidly (Turnbull 1968:132). Persons from other bands will be admitted as members for a variety of reasons, while others will just as easily leave for nearby bands. The dynamics of band life generates constant movement and flux. A band becomes "vulnerable to diminishing returns – so to a greater velocity of movement, or else to fission – in proportion to its size," claims Sahlins (1974:34). The more persons a band has to feed, the more rapidly it exhausts the food supply in the vicinity of the campsite, though that would not necessarily affect the more distant hunting grounds. Movement entails the transfer of all the members of the camp and their stores and implements, often including the carrying of burning embers to kindle the fire at the next camp (Turnbull 1961:58), the rebuilding of huts, and the exploration of the new neighborhood. But a band also needs enough people to take care of non-working dependents, who seem to amount to up to a third of the members (Sahlins 1974:21), to protect members against intruders, such as tigers and elephants, and to mount a hunt with nets (Turnbull 1961:91). The dilemma of wanting to keep the band small, as against the advantage of increasing its size, is a constant feature of life in bands. Thus, Turnbull begins the account of his sojourn with the Mbuti Pygmies with the description of a band of three extended families camping in a circle, with another extended family camping nearby in a separate circle (Turnbull 1961, illustration on p. 32). These people seek to become full members of the band, and try to prove their case, among other things, by ruining a net-hunting expedition to which they were not invited. At the end of Turnbull's stay, however, they were about to become full members and were expected to join the main camp at its next move (1961:249). The two amoebas were fusing completely. But there were also times when the camp would split up into smaller units, each going its own way, for instance in search of honey (1961:237).

As the economic activities of hunter-gatherers require only a few hours of daily labor, they appear to have spare time on their hands. We hear that they spend it in "resting in camp, [women] doing embroidery, visiting other camps and entertaining visitors from other camps ... and especially [men] dancing" (Lee 1968:37; see also Eibl-Eibesfeldt 1972:72–79; Thomas 1958:73), or in celebrating elaborate rituals lasting several months (Turnbull 1961:132 ff.; Silberbauer 1965:22). What appears to be "leisure" is really prime time devoted to *sociability*, the play-form of living together, where the immediate "aim is nothing but the success of the sociable moment" (Simmel 1964:45). Although part of the game is that people put a pleasant face on it, it is an obligatory and often strenuous activity. But the results are well worth the effort. "Something wonderful had come into our lives and filled them with the magic of love and trust" notes Turnbull (1961:144) at the end of an extended ritual. Sociability work puts the members of the band at ease with one another and engenders mutual trust. It creates a medium that envelops the members and assures them of the unfailing support of the group. This allows them to cooperate in communal activities as well as in specific task groups. It is also the basis of common moral standards and of social control. A member who fails to live up to the standards set by the group becomes the butt of gossip. If the offense is more severe, he or she is excluded from the sharing of food and in extreme cases may even be forced to leave the camp (Turnbull 1961:100). Perhaps these practices account for "the way everything settles itself with apparent lack of organization" (Turnbull 1961:115) among the Mbuti Pygmies and in other band societies.

The analysis of bands may have far-reaching implications for theories of early human territoriality and migration. I have argued that territoriality, in the sense of claims to numerous rights in land and the resources it harbors, does not serve the interests of the bands. Yet people do form an attachment to a region, because in the course of their sojourn they learn so much about it. They become used to the sources of food, raw materials, and camping sites it provides and learn to cope with the dangers lurking in it, and that makes it convenient to stay on. Thus, they become habituated to the area; it becomes their "habitation," their place of residence. But the Mbuti do not consider the land as their own. They rather insist that ownership is vested in the gods of the region, personified as "the forest," the source of all the good and bad it offers (Turnbull 1965:253), a belief that allows them to use all the forest's resources, wherever they may be found.

People reside in an area only as long as the going is good. When its resources are depleted, they move away and others will later on take their place. Each shift of camps is of very limited scope. Yet people may in the course of time cover great distances, because of an innate tendency to move around and seek knowledge. Every member of a camp explores the vicinity for new possibilities and resources, and hunters may roam over large areas in their search of prey. Thus, Hewlett (1996:223) reports that among African Pygmies the average net hunt covers 8 to 15 km, the average bow-and-arrow hunt 7 to 8 km, while spear hunts for elephants involve "very long hours and great distances." While bands seem at any particular moment to be confined to a home region, they may over time move gradually and almost imperceptibly into new areas.

Assuming that in Acheulian times there were no settled peoples or territorial groups, there was nothing to stop bands from moving. A group that appeared in the short run to live in a stable habitat may in the long run have moved into a new region. For illustrative purposes let us find out how long it would take a band to cover the 4,200 km from Olduvai Gorge to Gesher Benot Ya'aqov, assuming that it moves no more than an (absurdly small) average of 100 m a year. At such a slow but constant rate, it would have covered the distance in a mere 42,000 years, a small segment of the Acheulian period.

Conversely, we may safely argue that in such band societies the moves of camps were slow and difficult. People's attachment to an accustomed and abundant environment, the many dependants and other encumbrances on free movement, the expected realignment of camp members at each move, all these tended to slow down movement. It is therefore unlikely that there ever were isolated episodes of rapid long-distance migration of populations out of Africa, as Bar-Yosef & Belfer-Cohen (2001) argue. Instead, one might think about a steady and uncoordinated flow of slow-moving bands going off in different directions, following the variable dictates of the environment. In a study of gene flow in modern baboons, Simmons found "sporadic, but continuing multi-directional migrations and gene flow" (Simmons 1999:107). She believes that these findings may be applied to migrations of hominids in the Levantine Corridor in the Late Pleistocene. These findings seem to support a model of "numerous repeated episodes of multi-directional migrations and gene flow" (Simmons 1999:101), which could fit a model of numerous bands responding to environmental changes, moving slowly and in many directions through the land.

In this article I have tried to develop a reasonably complex model of Acheulian society, with an emphasis on group formation. I expect that when the model is tested in the field it will be found wanting. After all, by being falsified it would prove its scientific worth. For the time being, the model is sustained mainly by its methodology and internal logic, and to a lesser extent by ethnographic accounts and relatively recent archaeological data. This should change in the future, as more and more Acheulian sites are discovered and explored. We must expect to find considerable diversity in sites belonging to the same period, and even greater changes over time. The stereotyped notion that Acheulian culture is static, often called the "Acheulian enigma," will then be finally laid to rest.

Acknowledgments

My belated concern with prehistoric man needs an explanation. It began in 2000, when Naama Goren-Inbar invited me to join a study group on "Human Paleoecology in the Levantine Corridor" at the Hebrew University's Institute for Advanced Studies (held in 2002). I hesitated, knowing that paleoecology was a complex and rapidly developing science and that any work in this field demanded painstaking preparation. But Naama assured me that she and her colleagues would give me all the help needed. So I took the plunge and began to prepare myself by studying texts in paleoanthropology. I soon realized how little was known about Acheulian society. However, I felt that the study of small political groups, a theme that had engaged me during a study of the Negev Bedouin (Marx 1967), could provide a point of entry. My first attempt was an essay on corporate descent groups, which I presented at a conference on "Primary Solidarity and Elite Groups," at the Jewish-Arab Center, Haifa University, in July 2001. The participants at the conference, and particularly Dale Eickelman, who offered very detailed comments, encouraged me to continue the quest. In an article that grew out of this paper, I argue that corporate groups are not only varied and ubiquitous, but are also one of the most common forms of human interaction. Corporate descent groups are only one type of corporate group, and not necessarily the most important one (Marx n.d.). The present article continues from that point and applies the findings to the Acheulian. The members of the study group, Naama Goren-Inbar, Shoshana Ashkenazi, Craig Feibel, Mordechai Kislev, Bo Madsen, and François Valla, all gave me a helping hand and proffered many useful suggestions. Anna Belfer-Cohen and Erella Hovers gave me many incisive and useful comments, for which I am deeply grateful. I thank the Institute for Advanced Studies and its staff for providing a caring environment and excellent conditions for scholarly work.

References

Abu-Rabia, A. (1994). *The Negev Bedouin and Livestock Rearing: Social, Economic and Political Aspects*. Oxford: Berg.

Aswad, B. C. (1971). *Property Control and Social Strategies in Settlers in a Middle Eastern Plain*. Ann Arbor: Museum of Anthropology, University of Michigan.

Barnard, A. (1979). Kalahari Bushman settlement patterns. In (P. C. Burnham & R. F. Ellen, Eds.) *Social and Ecological Systems*. London: Academic Press, pp. 131–144.

Barnard, A. (1992). *Hunters and Herders of Southern Africa: A Comparative Ethnography of the Khoisan Peoples*. Cambridge: Cambridge University Press.

Bar-Yosef, O. & Belfer-Cohen, A. (2001). From Africa to Eurasia – early dispersals. *Quaternary International* **75**, 19–28.

Beck, L. (1991). *Nomad: A Year in the Life of a Qashqa'i Tribesman in Iran*. London: Tauris.

Befu, H. & Plotnicov, L. (1962). Types of corporate unilineal descent groups. *American Anthropologist* **64**, 313–327.

Bird-David, N. (1992). Beyond "The Original Affluent Society": A culturalist reformulation. *Current Anthropology* **13**, 25–47.

Bloch, M. (1953). *The Historian's Craft*. New York: Knopf.

Blurton Jones, N. G., Hawkes, K. & O'Connell, J. F. (1996). The global process and local ecology: How should we explain differences between the Hadza and the !Kung? In (S. Kent, Ed.) *Cultural Diversity among Twentieth-century Foragers: An African Perspective*. Cambridge: Cambridge University Press, pp. 159–187.

Boas, F. (1966). *Kwakiutl Ethnography* (H. Codere, Ed.). Chicago: University of Chicago Press.

Buchler, I. R. & Selby, H. A. (1968). *Kinship and Social Organization: An Introduction to Theory and Method*. New York: Macmillan.

Colchester, M. (1984). Rethinking stone age economics: Some speculations concerning the Pre-Columbian Yanoama economy. *Human Ecology* **12**, 291–314.

Dunbar, R. I. M. (1996). *Grooming, Gossip and the Evolution of Language*. Cambridge, MA: Harvard University Press.

Early, E. A. (1993). *Baladi Women of Cairo: Playing with an Egg and a Stone*. Boulder, CO: Lynne Rienner.

Eibl-Eibesfeldt, I. (1972). *Die !Ko-Buschmann-Gesellschaft: Gruppenbindung und Aggressionskontrolle bei einem Jäger- und Sammlervolk*. Munich: Piper.

Eickelman, D. F. (1989). *The Middle East: An Anthropological Approach*. 2nd Edition. Englewood Cliffs, NJ: Prentice-Hall.

Engels, F. (1972) [1884]. *The Origin of the Family, Private Property and the State in the Light of the Researches of Lewis H. Morgan* (E. B. Leacock, Ed.). London: Lawrence and Wishart.

Fortes, M. (1970). *Kinship and the Social Order: The Legacy of Lewis Henry Morgan*. London: Routledge and Kegan Paul.

Fried, M. H. (1957). The classification of corporate unilineal descent groups. *Journal of the Royal Anthropological Institute* **87**, 1–29.

Gerber, H. (1993). Musha'. *Encyclopaedia of Islam, New Edition. Vol. 7*, pp. 666–667.

Goren-Inbar, N., Lister, A., Werker, E. & Chech, M. (1994). A butchered elephant skull and associated artifacts from the Acheulian site of Gesher Benot Ya'aqov, Israel. *Paléorient* **20**, 99–112.

Goren-Inbar, N., Sharon, G., Melamed, Y. & Kislev, M. (2002). Nuts, nut cracking and pitted stones at Gesher Benot Ya'aqov, Israel. *Proceedings of the National Academy of Sciences USA* **99**, 2455–2460.

Hawkes, K., O'Connell, J. F. & Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Current Anthropology* **38**, 551–577.

Hayden, B. & Cannon, A. (1982). The corporate group as an archaeological unit. *Journal of Anthropological Archaeology* **1**, 132–158.

Hewlett, B. (1996). Cultural diversity among African pygmies. In (S. Kent, Ed.) *Cultural Diversity among Twentieth-century Foragers: An African Perspective*. Cambridge: Cambridge University Press, pp. 215–244.

Hüsken, T. & Roenpage, O. (1998). *Jenseits von Traditionalismus und Stagnation: Analyse einer beduinischen Ökonomie in der Westlichen Wüste Ägyptens*. Berlin: Lit.

Ingold, T., Riches, D. & Woodburn, J. (Eds.) (1991). *Hunters and Gatherers, Vols. 1 and 2*. Oxford: Berg.

Isaac, G. Ll. (1986). Foundation stones: Early artifacts as indicators of activities and abilities. In (G. N. Bailey & P. Callow, Eds.) *Stone Age Prehistory: Studies in Memory of Charles McBurney*. Cambridge: Cambridge University Press, pp. 221–240.

Jakubowska, L. (1992). Resisting "ethnicity": The Israeli State and Bedouin identity. In (C. Nordstrom and J. A. Martin, Eds.) *The Paths to Domination, Resistance, and Terror*. Berkeley: University of California Press, pp. 85–105.

Kent, S. (1996). Hunting variability at a recently sedentary Kalahari village. In (S. Kent, Ed.) *Cultural Diversity Among Twentieth-century Foragers: An African Perspective*. Cambridge: Cambridge University Press, pp. 125–156.

Klein, R. G. (with Edgar, B.) (2002). *The Dawn of Human Culture*. New York: Wiley.

Kressel, G. M. (1996). *Ascendancy through Aggression: The Anatomy of a Blood Feud among Urbanized Bedouin*. Wiesbaden: Harrassowitz.

Lee, R. B. (1968). What hunters do for a living or how to make out on scarce resources. In (R. B. Lee & I. DeVore, Eds.) *Man the Hunter*. Chicago: Aldine, pp. 30–48.

Lee, R. B. (1972). !Kung spatial organization: An ecological and historical perspective. *Human Ecology* **1**, 125–147.

Lee, R. B. (1984). *The Dobe !Kung*. New York: Holt, Rinehart and Winston.

Lee, R. B. & I. DeVore (Eds.) (1968). *Man the Hunter*. Chicago: Aldine.

Lewin, K. (1951). Defining the "field at a given time." In (D. Cartwright, Ed.) *Field Theory in Social Science: Selected Theoretical Papers*. New York: Harper, pp. 43–59.

Madsen, B. (2003). *The Cutting Edge: A Million Years of Stone Technology*. Jerusalem: Hebrew University, Institute of Archaeology (DVD).

Maine, H. (1917) [1861]. *Ancient Law*. London: Dent.

Marshall, L. (1976). Sharing, talking and giving: Relief of social tensions among !Kung Bushmen. In (R. B. Lee & I. DeVore, Eds.) *Kalahari Hunter-Gatherers: Studies of the !Kung San and their Neighbors*. Cambridge, MA: Harvard University Press, pp. 349–371.

Marx, E. (1967). *Bedouin of the Negev*. Manchester: Manchester University Press.

Marx, E. (1980). On the anthropological study of nations. In (E. Marx, Ed.) *A Composite Portrait of Israel*. London: Academic Press, pp. 15–28.

Marx, E. (1987). Relations between spouses among the Negev Bedouin. *Ethnos* **52**, 156–179.

Marx, E. (n.d.). Corporate descent groups and other corporate groups (in preparation).

Meillassoux, C. (1981). *Maidens, Meal and Money: Capitalism and the Domestic Community*. Cambridge: Cambridge University Press.

Moore, S. F. (1978). *Law as Process: An Anthropological Approach*. London: Routledge and Kegan Paul.

Morgan, L. H. (1974) [1877]. *Ancient Society or Researches in the Lines of Human Progress from Savagery through Barbarism to Civilization*. Gloucester, MA: Peter Smith.

Peletz, M. G. (1995). Kinship studies in late twentieth-century anthropology. *Annual Review of Anthropology* **24**, 343–372.

Peters, E. L. (1990). *The Bedouin of Cyrenaica: Studies in Personal and Corporate Power* (J. Goody & E. Marx, Eds.). Cambridge: Cambridge University Press.

Peterson, N. (1979). Territorial adaptations among desert hunter-gatherers: The !Kung and Australians compared. In (P. Burnham & R. F. Ellen, Eds.) *Social and Ecological Systems*. London: Academic Press, pp. 111–129.

Rugh, A. B. (1997). *Within the Circle: Parents and Children in an Arab Village*. New York: Columbia University Press.

Sahlins, M. (1974). *Stone Age Economics*. London: Tavistock.

Schebesta, P. (1928). *Among the Forest Dwarfs of Malaya*. London: Hutchinson.

Schneider, D. M. (1968). *American Kinship: A Cultural Account*.

Englewood Cliffs, NJ: Prentice-Hall.

Simmel, G. (1964). *The Sociology of Georg Simmel* (K. H. Wolff, Ed.). Glencoe, IL: Free Press.

Silberbauer, G. B. (1965). *Report to the Government of Bechuanaland on the Bushman Survey*. Gaborones: Bechuanaland Government.

Silberbauer, G. B. (1996). Neither are your ways my ways. In (S. Kent, Ed.) *Cultural Diversity among Twentieth-century Foragers: An African Perspective*. Cambridge: Cambridge University Press, pp. 21–64.

Simmons, T. (1999). Migration and contact zones in modern human origins: Baboon models for hybridization and species recognition. *Anthropologie* **37**, 101–109.

Smith, M. G. (1974). *Corporations and Society*. London: Duckworth.

Sollas, W. J. (1911). *Ancient Hunters and their Modern Representatives*. London: Macmillan.

Thomas, E. M. (1958). *The Harmless People*. New York: Random House.

Turnbull, C. M. (1961). *The Forest People*. London: Jonathan Cape.

Turnbull, C. M. (1965). *Wayward Servants: The Two Worlds of the African Pygmies*. New York: Natural History Press.

Turnbull, C. M. (1968). The importance of flux in two hunting societies. In (R. B. Lee & I. DeVore, Eds.) *Man the Hunter*. Chicago: Aldine, pp. 132–137.

/Useb, J. (2001). "One chief is not enough!": Understanding San traditional authorities in the Namibian context. In (A. Barnard & J. Kenrick, Eds.) *Africa's Indigenous Peoples: "First Peoples" or "Marginalized Minorities"?* Edinburgh: Centre of African Studies, University of Edinburgh, pp. 15–29.

Valla, F. (2000). La sédentarisation au Proche Orient: La culture Natoufienne. In (J. Guilaine, Ed.) *Premiers Paysans du Monde: Naissances des Agricultures*. Paris: Editions Errance, pp. 13–30.

Van Velsen, J. (1967). The extended-case method and situational analysis. In (A. L. Epstein, Ed.) *The Craft of Social Anthropology*. London: Tavistock, pp. 129–149.

Weber, M. (1947). *The Theory of Social and Economic Organization*. London: Hodge.

Woodburn, J. (1980). Hunters and gatherers today and reconstruction of the past. In (E. Gellner, Ed.) *Soviet and Western Anthropology*. New York: Columbia University Press, pp. 95–117.

Woodburn, J. (2001). The political status of hunter-gatherers in present-day and future Africa. In (A. Barnard & J. Kenrick, Eds.) *Africa's Indigenous Peoples: "First Peoples" or "Marginalized Minorities"?* Edinburgh: Centre of African Studies, University of Edinburgh, pp. 1–14.

Wynn, T. (1995). Handaxe enigmas. *World Archaeology* **27**, 10–24.

Chapter VIII

Culture and Genes in the Evolution of Human Language

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Abstract

This paper presents a theoretical model of the evolution of human language in which genetic evolution follows, rather than precedes, cultural evolution. According to the model, a process which started with the cultural evolution of linguistic communication gradually unmasked genetic variations within hominid populations and ended up with partial genetic assimilation of a whole host of learning capacities, some of which were specifically linguistic. As we show, this process of cultural-genetic co-evolution may have contributed to the gradual sophistication of the linguistic system, in terms of its cognitive-semantic categories, and to the establishment of language as a major system of social interaction. The paper also discusses the possible role of ciphering in the co-evolution of language and the question of the possible time-frame for this evolutionary process.

Introduction

In the last fifteen years, a considerable number of scholars have formulated hypotheses concerning the evolution of human language (e.g., Corballis 1991; Donald 1991; Lieberman 1991; Bickerton 1995, 2002; Dunbar 1996; Deacon 1997). The theoretical and empirical evaluation of these hypotheses is a very problematic matter. Not only is there no fossil evidence that can unambiguously indicate when language first emerged, but even what we seem to know about the evolution of archaic *Homo sapiens* from *Homo erectus*, and about the evolution of modern *Homo sapiens sapiens*, is beset with interpretative hurdles. For example, what is the relationship between the complexity of the tools found in the Middle Paleolithic and linguistic ability, and what can this tell us about human symbolic abilities (Ohnuma et al. 1997)? Did language emerge gradually or was it the result of a single (or a very few) saltatory event? What should we assume about the linguistic abilities of our late *erectus* ancestors with their large brains (1000–1200 cc) and their complex culture in view of the fact that bonobo chimpanzees, with a brain volume of 500 cc, can be taught simple language (Savage-Rumbaugh et al. 1998)? What was the modality in which language was first expressed (gestural, vocal, or both)? These are just a few of the questions that linguists, anthropologists, and cognitive scientists interested in the evolution of humans ask. Different evolutionary hypotheses suggest different answers to all or some of these questions.

Evolutionary scenarios may focus on the question of the trait's origin or on the question of the process of its evolution from some arbitrary stage, when it was already present in a rudimentary but recognizable form. In the latter case, the stress is on the sophistication and the elaboration of the trait, rather than its actual primary emergence, and it is on this aspect of the evolution of language that we shall focus. However, even hypotheses that avoid the "origin question" cannot avoid presenting the authors' assumption as to what constitutes the major cognitive and social pre-adaptations that allow their particular scenario to occur, and we shall therefore refer to them briefly. We shall then present a brief summary of our co-evolutionary view of language evolution (Dor & Jablonka 2000, 2001), and discuss a few theoretical issues having to do with the role of language in the construction of social world views, the role of ciphering in the evolution of language, and the question of the time frame of language evolution.

The evolution of language: The cultural engine

Various questions may be asked about the evolution of human language, and the different evolutionary hypotheses attempt to emphasize and address different aspects of these questions. Some scholars attempt to deal with the types of selection pressures that played a role in the evolution of language – those ecological and social settings that may have rendered linguistic communication both beneficial and likely to emerge. Thus, for example, Dunbar (1996) suggests that an increase in group size led to immense pressure on the management of personal-social relationships, which led to a new (linguistic) form of communicative exchange. Another such example is Miller's (2000) theory, in which language is assumed to have been used as an indicator of a mate's quality, and its evolution is explained in terms of sexual selection. A different type of approach, exemplified by the works of Jackendoff (1999), Aitchison (1996), and Bickerton (1995), focuses on the delineation of the possible stages in the process of language evolution, trying to draw a reasonable line of progression, without explicitly addressing the selection pressures underlying each stage. The stages suggested reflect the authors' conception of the structure of language on the one hand, and their assumptions concerning the rate of evolution on the other hand: Jackendoff and Aitchison opt for an essentially gradual evolutionary process, while Bickerton suggests a major saltatory stage. A third approach focuses on the nature of the dynamics of the evolutionary process. Kirby (2000), for example, provides a simulation model in which syntactic regularities spontaneously emerge in a social setting where individuals agree on a set of meanings (this model does not deal with the genetic aspect of the evolutionary process).

In our own work (Dor & Jablonka 2000, 2001), we concentrate on the dynamics of the evolutionary process and suggest that it was determined by a specific type of interaction between *cultural evolution* and *genetic evolution* – an interaction that is underlined by a process of *partial genetic assimilation*. We claim that both individual selection and group selection (of the type discussed by Boyd & Richerson 1990, and Henrich & Boyd 1998) have played an important role in this process.

Our model takes as its starting point an arbitrary moment in evolutionary history, when a group of hominids reached the stage in which the members of the group shared what we think of as the necessary cognitive precursors for linguistic communication. They had some preliminary form of a *theory of mind* (the ability to attribute beliefs and desires to other individuals); they were capable of *social conceptualization*, including the implicit understanding of social relations and hierarchies; and they were motivated to share information when living, as they did, in a world full of uncertainties. Sharing information through social learning in a small group is a potentially very advantageous activity; it has kin-related benefits in the family setting and more general benefits of vital information exchange concerning food and dangers beyond the family nucleus.

At this early stage, our community of hominids used a relatively simple communication system. Certain vocalizations represented a constrained set of meanings. The meanings and their markers were probably different from those we use in present-day languages. They included, for example, some conventionalized alarm-calls, some imitations of animal sounds that were used as referents to those animals or their behavior, emotional-social vocalizations that had become controlled voluntarily and were used as referential lexical items in certain situations, and so on. This communication system may be thought of as containing some of the components that are found today in the communication systems of vervet monkeys (reviewed in Hauser 1997), dwarf mongooses (Rasa 1985), killer whales (Rendell & Whitehead 2001), and chimpanzees in the wild (Whiten et al. 2001).

What was the expressive power of this rudimentary communication system? Obviously, it could express a set of meanings much narrower than that of fully-fledged human languages. For our present purposes, however, the more significant assumption is that the communication system could express much less than what its users could represent conceptually. In other words, individuals at this stage were capable of thinking and feeling much more than they could express. This, to be sure, seems to be true for all stages of language evolution, including our own, and has been dramatically demonstrated in experimental settings involving chimpanzees and young children (Savage-Rumbaugh & Levin 1994).

We further assume that individuals at this stage used their quasi-linguistic system readily and naturally, and that their children readily acquired it. Inevitably, the genetic constitution of the community that allowed for the acquisition and use of the linguistic system was variable, with some individuals being better at acquiring and using the system than others. However, all members of the group are assumed to have been able to acquire and use the linguistic system, and the genetic differences between individuals at this stage did not translate into consistent corresponding differences in reproductive success.

With this state of affairs as our background, we assume a steady and persistent process of cultural evolution, a process not unlike any other process of cultural development. At various times individuals or groups of individuals came up with different types of linguistic innovations. Most innovations probably took place again and again, and many were quite transient. At first, most innovations probably consisted of new lexical items with specific referential meanings (new "words") and new discourse markers and pragmatic conventions for linguistic communication (e.g., conventions of speech-acts); later on, some innovations probably consisted of new markers for novel conceptual distinctions (e.g., a marker for the plural form). Some of these innovations may have been accidental, and some may have been the result of conscious effort or of social play. They were probably initiated by individuals who were clever enough, or explorative, or just lucky, and happened to be in the right social context at the right time. Some of the innovators may have been inquisitive youngsters and, in some cases, the innovation may have been the result of interactions within the group, either in a sub-group (of men, women, or juveniles), or in special but regular settings where different groups met and communicated (e.g., for trade or ritual purposes). The main social driving force for the innovations was the pressure for better communication within the group and, to a lesser extent, between groups. This pressure may have been causally related to a whole host of processes: an increase in group size (Dunbar 1996); significant changes in ecological conditions, requiring greater group stability and cooperation (Bickerton 2002); changes in tool usage that benefited from linguistic instruction; or changes in the patterns of migration or interaction between different hominid populations. Different combinations of causal factors may have been involved in each particular case. Crucially, however, we do not need to invoke a genetic explanation for any of the innovations: the linguistic innovations of this stage were within the genetically based cognitive capacity of their inventors.

Among the different innovations, those which had the best chance of establishing themselves as part of the linguistic arsenal of the group were probably those that were not too remote from the existing cognitive and linguistic world and could therefore be learned by at least some of its members. Although only a small minority in any community is capable of real innovation, a much larger group of individuals is capable of learning the innovation (understanding and using it) once it is there. And again, there is no need to invoke a genetic explanation for the dissemination of the innovation; hominid cognition is extremely plastic, and social learning takes advantage of this plasticity. Moreover, research on the acquisition of language in children and chimpanzees teaches us that at every developmental stage, individuals' achievements in linguistic *comprehension* are much more advanced than their achievements in linguistic *production*. An innovator thus has a good chance of being understood, especially by those individuals who are close to him or her – family members and close friends.

Once an innovation was learned by a few members of the community, its fate depended to a significant degree on its propagation and dissemination across the population. These, in turn, probably depended upon a large set of considerations, including the functional significance of the innovation, the social status of the innovator and the first learners, the level of social cohesion within the first subgroup of learners, and so on. We may assume that in the innovator's own generation, the propagation of the new linguistic tool was unstable and uncertain. Many innovations, including some very useful ones, probably disappeared at this stage. One reason for this is that the value of many innovations could be fully appreciated only when they came to be used by a significantly large and cohesive group of communicators (there is positive frequency-dependent selection, up to a point, at least). We may, however, assume that the innovation had a better chance of establishing itself after the first learners transmitted it to their offspring, because children seem to play a significant role in the establishment of cultural traditions. For example, juveniles played a major role in the establishment of the food washing cultural habit in the Japanese macaques of Koshima Island (Avital & Jablonka 2000). We may also assume that for a long time, after the original invention, the innovation itself went through a process of cultural development. It may have been improved and made easier to learn, and it may have become conventionalized and streamlined in a long dynamic process of learning and re-learning (Kirby 2000).

Obviously, the chances of an innovation establishing itself depended crucially on its value as a tool of social communication. For an innovation to survive, its usage would have to have been beneficial for the speakers who decided to adopt it. In general, the adaptive value of a linguistic innovation is a direct function of how much information it allows one to convey, and an inverse function of how difficult it is to learn, remember, and display (Sperber & Wilson 1986). The information potential of an innovation does not necessarily have to be related to practical considerations such as improving the efficiency of cooperation in hunting or fighting, or sharing information about the natural environment. Although these considerations are important, the information potential of an innovation is always a social issue: it has to do with the sharing of social information (social relations, social events, and social hierarchies), with the sharing of social narratives and myths, and with the construction of social epistemology (Knight 1998; Heeschen 2001). The construction of social epistemology (e.g., the specific ways in which the group members classify events and causes) plays an important role in linguistically based social identity, strengthening the adaptive value of the innovation to an additional degree.

For a linguistic innovation to propagate, it has to survive for a sufficient amount of time, and preferably in a wide array of changing circumstances. This is especially important in the development of markers for semantic categories (such as plurality and singularity, tense, gender, animacy, and so on). New lexical items may come and go, depending on circumstances, but categorical markers, which refer to general and stable aspects of the perceived world (e.g., plurality and gender) are likely to survive social changes over long periods of time. Additionally, linguistic innovations had to meet conditions set by psychological constraints, by the pre-linguistic mind-set of the hominids. In the first place, innovations which corresponded to pre-existing cognitive or developmental biases were the ones most easily learned, remembered, and transmitted, and hence were more likely to be selected (Deacon 1997; Sperber 1996).

A second type of system constraints is that imposed by the already established linguistic system; the innovation has to fit into the existing framework. This means that, at least from a certain point in the evolution of language, the system itself dictated the direction of its own future evolution. Moreover, as the system became more complex, it gradually set more and more constraints on its own ability to go through major changes. Thus, although fully-fledged languages as we know them are very flexible, the basic grammatical categories of human languages may not be expanding today at the rate they did during the early hominid period. Moreover, some types of information, such as emotional messages or manual instructions, were probably very effectively communicated by non-linguistic means, such as body language, facial expressions, mime, song and dance, and so on. Therefore, linguistic innovations directed at these types of information did not survive (or may have not been invented in the first place), because the other means of communication rendered them unnecessary. Thus, division of labor between the different systems of communication may have had a significant role in the cultural evolution of the highly constrained expressive envelope of language.

Let us assume, then, that some of the adaptive linguistic innovations of the first stages managed to spread and establish themselves in the community. These innovations could have been very enduring, because they were both dependent upon, and constitutive of, the social structure, and because social traditions are, by their very nature, self-perpetuating. This cultural change enhanced the communicative capacity of individuals within the community, thus increasing the (culturally determined) fitness of the best individual communicators, as well as the fitness of the entire group.

Crucially, however, the establishment of the innovations also raised the demands for *social learning* imposed on individuals in the community. They had to acquire the new innovations in order to be able to participate in social communication. Moreover, linguistic innovations constructing sharp categories meant that individuals had to learn to look at the world in new ways, direct attention to new aspects of reality, process and remember new types of information, and so on. In short, the linguistic innovations which established themselves in the community *changed the social and epistemic niche* in which the individuals lived, and they had to adapt to it. Thus, for example, linguistic communication allows for the gradual move from a holistic or analogue representation of the world to a more discrete or digital one, in which conceptual distinctions are much more sharply made. This was no doubt a great conceptual challenge to individuals in the crucial period in which this change took place. In adapting themselves to innovations of this type, individuals could at first count on the built-in residual plasticity of their minds. Those individuals, and cohesive groups of individuals, who made better use of the innovations for efficient communication (for whatever cultural or social reason) probably benefited; they were more likely to thrive.

The genetic side of the coin: Partial genetic assimilation

As we have said, the new innovations exposed new types of differences between individuals. Some individuals understood the innovation better than others; some learned to use it themselves, others managed to passively comprehend; some others may have not been able to keep up with it. At least some of this exposed variability had to do with the individuals' genetic make-up. Up to a point, this genetic variability in linguistic competence did not translate into differences in fitness; for example, individuals may have compensated for the difficulties in other ways. However, with the accumulation of the linguistic innovations and with the increased social dependence on language and the niche that it constructed, the previously selectively neutral genetic variation began to be selectively important. Plasticity was gradually stretched, and individuals found the accumulating linguistic task more and more demanding.

The period in which genetic differences in the potential to understand and use linguistic innovations was not important may have lasted a long time. Eventually, however, after a long period of consistent, directional cultural selection, genetic differences began to make a consistent difference to reproductive success: some individuals failed to thrive in the increasingly linguistic culture; others survived; still others did particularly well. The frequencies of those gene combinations that contributed to easier language acquisition and usage increased in the population. Eventually, after a period of this type of selection, the community consisted of individuals whose general genetic make-up was such that the adults used the more sophisticated linguistic system more or less comfortably, and the children comfortably acquired it. Acquiring and learning the language was quicker and required less effort. Once this happened, it allowed for the whole process to start all over again: individuals were "freed" to make use of their cognitive plasticity, to invent and learn more linguistic innovations, and so on. (Of course, thinking in terms of discrete cultural and genetic *stages* is an idealization; the process was obviously continuous.)

The process just described, in which genetic changes are guided by a process of learning, is known in the genetic literature as *genetic assimilation* or the *Baldwin effect* (for recent evaluations and discussions of the Baldwin effect, see Weber & Depew 2003). It describes the transformation, through Darwinian selection, of a learned response into a more genetically fixed or "instinctive" response. When faced with a new challenge in their environment (e.g., a new predator, or a new set of cultural innovations), individuals first adapt to the challenge by *learning*. If the selective pressure is consistent and ongoing, and if the necessary learning process is lengthy and costly, individuals will be selected for their ability to respond appropriately to the challenge without the full investment in the learning process. In other words, individuals who learn more rapidly and efficiently, who are more "instinctive" responders to the challenge, will be selected.

The transition from learned to more "instinctive" or "innate" response can be the result of new mutations, which accumulated while the population adapted to the new challenge through learning, and this was indeed how the process was first envisaged (Baldwin 1896). However, C. H. Waddington (1953), the British geneticist and embryologist, showed that new mutations are not necessary because the transformation can occur through the formation of new combinations of genes following sexual reshuffling and continuous exposure to the selective environment. Moreover, the transition to "innate" responses can occur not only for behavioral, learned traits, but also for physiologically induced traits; it can explain, for example, why human babies are born with thickened skin on the soles of their feet before they ever walk a step (for a more detailed exposition of Waddington's experimental and theoretical framework, see Avital & Jablonka [2000] and Dor & Jablonka [2000]).

Waddington's approach has been applied to the evolution of behavioral instincts. Thus, for example, the innate fearful reaction of many small mammal and bird species to hissing snake-like noises (Edmunds 1974), and the fearful reaction of naive spotted hyena cubs to the smell of lions (Kruuk 1972), may be explained as assimilated responses. In all these cases, individuals were selected on the basis of their ability to learn to respond to the particular stimulus. The individuals who survived and reproduced were those who managed to learn to respond adaptively on the basis of a minimal number of trials. In some cases, after many generations of selection, some individuals could even respond to the stimulus after a single exposure. In these cases, we say that the learned response became "innate" In all cases, however, it is *the ability to learn to respond to the stimulus* that was selected: throughout the process, learning became more and more efficient and rapid, sometimes even reaching the point where it was "internalized."

Crucially, most assimilation processes do *not* end with a completely internalized, instinctive response. Usually, the assimilation process will be *partial*: it will significantly reduce the amount of learning needed, and although learning will be still be needed to some extent, it will be much more rapid and efficient (Hinton & Nowlan 1987; Behera & Nanjundiah 1995). The speed of assimilation is expected to vary in different cases, depending on the intensity of selection, the number of genes involved, and the nature of their interactions. This has an interesting consequence for the evolution of linguistic categorization:

whereas a fully assimilated response associates the response (e.g., a type of grammatical marking) with a highly specific stimulus (e.g., an experienced situation), partial assimilation results in the association of the response with a larger, and much more diffuse, set of stimuli, which includes all the stimuli that are similar enough. It thus associates a response (in our case, a specific pattern of linguistic behavior) with a *category* (such as goal-oriented activity; for more examples see Dor & Jablonka 2000).

Adaptation through learning thus defines the environment in which individuals operate. However, learning often also leads to the creation of *persistent* changes in the environment. Through their learned behavior, individuals construct the environment in which they live and in which they and their offspring are selected (Lewontin 1978; Odling-Smee et al. 1996). This makes selection more directional and more reliable, and enhances its effectiveness. A famous example of this process in humans is the evolution of lactose absorption following the domestication of cattle and the drinking of fresh milk (Durham 1991). As we have seen, the process of language evolution as we have described it consists of constant changes in the social environment – in the way individuals see the world and their place in it, and the way they communicate and cooperate.

Moreover, genetic assimilation may sometimes lead to the sophistication of behavior. When a behavior consists of a sequence of learned acts, and one of the acts in the sequence becomes genetically assimilated and no longer requires much learning, the sequence as a whole is learned more rapidly. It is then easier for an additional learned act to be added to it. It is thus possible to gradually extend and sophisticate the sequence of acts without changing the capacity to learn: genetically assimilating some previously learned behaviors "frees" the individual to learn additional acts, without extending the limits set by his or her learning capacity. This process, which involves the *assimilation* of a part of the behavioral sequence and the resulting *stretching* of the sequence by learning, is called the *assimilate-stretch* principle (Avital & Jablonka 2000). It may explain the evolution of many complex behavior patterns in nature and is likely to have been important in the evolution of linguistic capacity.

What kinds of traits could become genetically assimilated as humans developed language and became increasingly more dependent on it? It is probable that many aspects of general cognition were assimilated, to a certain degree at least, as suggested by Lieberman (1991), Donald (1991), Jablonka & Rechav (1996), Deacon (1997), and others. Individuals at later stages of such evolution were probably more intelligent, had better memories and better voluntary control of their sound production mechanisms, and were probably smarter social agents. We believe, however, that individuals at later stages had a cognitive constitution that was, in some significant ways, more biased towards the acquisition and usage of language than the cognitive constitution of individuals at previous stages. The process of partial genetic assimilation of capacities – which followed the long period of cultural evolution in which a community became more and more dependent on linguistic communication, and in which the survival of individuals depended to an increasing extent on their linguistic performance – must have targeted those cognitive capacities that were most useful for this specific type of behavior. Some examples are the capacity for recognizing discrete conceptual categories, for rapid processing of the speech channel, for recognizing linguistic-communicative intent, and for lexical memory. These are language-specific and must have been targeted by linguistically driven genetic assimilation.

This process of linguistically based genetic assimilation may actually have been related in an interesting way to the general evolution of human culture and human conceptualization. As we have already indicated, genetic assimilation also targeted general intelligence. We know, after all, that there was no strong constraint on the evolution of the hominids' general intelligence: hominid brains doubled in size in 2.5 million years. As the process of cultural and linguistic evolution constantly led to an extension of the environment as perceived by the community, individuals were constantly faced with more information about the world: they could learn more, and about more aspects of the world, because they could think and communicate more effectively. This created a process of positive feedback: the more individuals learned about the world, the more things they could communicate about; and the more things they could communicate, the more they could learn. On the one hand, the conceptual structures of individuals and the whole community evolved with the aid of the more complex communication tool – language. On the other hand, the evolution of conceptual structures, and general cognitive tools for learning, remembering, and so on, helped the concomitant evolution of the linguistic system. The linguistic system thus spiralled together with the conceptual system and with the motor control system. This wider spiral also included a wide variety of non-linguistic, culturally based evolutionary processes, which interacted with each other. The process resulted both in the expansion of hominids' conceptual capacities, and in the construction and expansion of their linguistic expressive envelope.

The above arguments suggest the notion that an important component of the evolution of language was group selection. Group selection occurs when the heritable variance among groups exceeds the heritable variance within groups (Sober & Wilson 1998). As language increases homogeneity within groups with respect to the transfer of information about important aspects of the group members' behavior, skills, and preferences, variance *among* different linguistic groups is consequently increased. The imposition of group identity, and the multi-generational sharing of information that occurred within groups, may have led to effective group selection of all group-associated traits, including language itself (Boyd & Richerson 1990; Henrich & Boyd 1998).

Some theoretical issues

In this section, we would like to make a few comments concerning some theoretical issues that arise naturally from the framework we have sketched. First, our framework, as well as that of others, is based on the assumption of information sharing in a group of hominids. As noted by many scholars, information sharing poses the general problem of the evolutionary stability of cooperation: it may be exploited by "free riders," who attempt to use the benefits (receiving valuable information) without paying the costs (reciprocating in information or in other ways). In small social groups, however, cooperation can be evolutionarily stable, despite the "free riders" problem, because of the benefits of kin selection, the benefits stemming from reciprocal altruistic acts between individual group members (as well as between small subgroups), and because of group benefits, mainly reducing the likelihood of group extinction. Indeed, stable cooperation and information sharing are found in social mammals such as mongooses, wolves, and bonobo chimpanzees (Avital & Jablonka 2000), and it is reasonable to assume that it was a feature of the life and communication of our ancestors.

Language, however, poses an additional problem within this context. Language is particularly prone to evolutionary instability, because linguistic messages are *cheap* and can therefore be easily used to convey false information (Knight 1998). This problem, we believe, is overstated. First, linguistic communication is multi-functional, and some of its most important functions cannot be reduced to the sharing of verifiable information: questions, requests, threats, ritualized stories, poems, and prayers are neither true nor false. Second, the socially oriented nature of linguistic communication, and what we assume about the cohesive nature of early human societies, may provide various effective types of control against systematic cheating. Linguistic gossiping, for example, allows for social control and surveillance, and hence for the imposition of sanctions and rewards. It is likely that this role of language more than compensates for its cheating potential in small intimate societies.

Knight (1998) makes the claim that language, which allows for easy cheating, thus allows for the construction of "collective lies" – sets of myths, practices, and belief systems which are socially controlled and create whole world-views for the group. This view is intimately related to an assumption that we make in our model – the assumption that one of the most important functions of linguistic innovations was their contribution to the developing epistemic niche of the community. Linguistic anthropological research (Gumperz & Levinson 1996) indicates that language does seem to have an impact on the way we conceptualize about the world around us, albeit in a more sophisticated way than that envisioned by Edward Sapir and Benjamin Lee Whorf, who first introduced the hypothesis of linguistic relativism at the beginning of the 20th century. Interestingly, Rappaport (1999) suggests that this aspect of language can also be used in a subversive manner, allowing for alternative world-views to emerge and compete. Thus, additional measures need to be taken by the community to control its epistemic space, and these measures sometimes take the form of "costly" religious rituals.

The fact that language allows effective social control suggests another aspect of its evolution, which to the best of our knowledge has not been hitherto explored: the possibility that social struggles for control led to the development of ciphering-related properties in language, and hence to the accentuation of the arbitrary features of language (at the cultural level) and to the increased cognitive plasticity (at the genetic level) that allows flexible transitions from one cipher to another, evolved with a double purpose: to allow for efficient, semantically based communication between selected interlocutors, and to make sure, at the same time, that outsiders do *not* have access to the communicated information. Thus, language evolved not just as a means of communication, but also, and importantly so, as a means of social differentiation and control. A simple thought experiment should make this hypothesis clear. Assume two interlocutors, A and B, who, for whatever reason, are invested in developing a communication system between them. The need to communicate, as such, should not necessarily result in a system manifesting the idiosyncratic properties of language. Assume, however, that we add a third agent, C, and that A and B are also invested in *not* sharing their information with C. In this case, some of the most important properties of language seem to make sense, including the *arbitrariness of the sign*, which is an absolutely necessary property of a ciphering system, because non-ciphering communication systems, which involve, for example, iconic communication, are relatively transparent.

Furthermore, focusing on the ciphering aspect of language naturally allows for the assumption of a constant social struggle (both between and within groups) between encipherers and decipherers, where the former constantly sophisticate the system, the latter constantly make an effort to "break the code," and so on. A social struggle of this type may trigger the cultural and genetic selection of those individuals whose cognitions are more suited for the invention, learning, and usage of rapidly changing codes. While the marking of fundamental semantic categories has led to the assimilation of some aspects of language, social linguistic games founded on changing codes have led to the evolution of plasticity at the less constant and more pragmatic levels of language acquisition and comprehension.

Finally, our framework allows for an educated guess concerning the time frame of language evolution. A common assumption is that syntactical language evolved with *Homo sapiens sapiens* or even later – that is, in a time frame of tens of thousands of years (e.g., Humphrey 1999). This leaves *Homo erectus* and archaic *Homo sapiens*, with their tool cultures, without syntactical language. Although this is not impossible (Donald 1991, for example, suggests that tool-culture was essentially mimetic), we think that there are good reasons to believe that language, including syntax, had an earlier origin. First, according to our model, the evolution of language was very gradual and very slow at both the cultural and the genetic levels. Second, the comparison with language-trained chimpanzees is illuminating in the following sense: chimpanzees seem to naturally have all the necessary preconditions for rudimentary language comprehension apart from the appropriate social context in which language can be learned. *Homo erectus* and archaic *Homo sapiens* were not inferior to bonobo chimpanzees in this respect, and seem to have lived in a very complex cultural environment. It is thus not implausible that the evolution of language spans a period starting with *Homo erectus*.

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References

Aitchison, J. (1996). *The Seeds of Speech: Language Origin and Evolution*. Cambridge: Cambridge University Press.

Avital, E. & Jablonka, E. (2000). *Animal Traditions: Behavioural Inheritance in Evolution*. Cambridge: Cambridge University Press.

Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist* **30**, 441–451, 536–553.

Behera, N. & Nanjundiah, V. (1995). An investigation into the role of genetic plasticity in evolution. *Journal of Theoretical Biology* **172**, 225–234.

Bickerton, D. (1995). *Language and Human Behaviour*. London: University College London Press.

Bickerton, D. (2002). Foraging versus social intelligence in the evolution of protolanguage. In (A. Wray, Ed.) *The Transition to Language*. New York: Oxford University Press, pp. 207–226.

Boyd, R. & Richerson, P. (1990). Group selection among alternative evolutionary stable strategies. *Journal of Theoretical Biology* **145**, 331–342.

Corballis, M. C. (1991). *The Lopsided Ape*. New York: Oxford University Press.

Deacon, T. (1997). *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: W. W. Norton.

Donald, M. (1991). *Origins of the Modern Mind*. Cambridge, MA: Harvard University Press.

Dor, D. & Jablonka, E. (2000). From cultural selection to genetic selection: A framework for the evolution of language. *Selection* **1**, 33–55.

Dor, D. & Jablonka, E. (2001). How language changed the genes: Towards an explicit account of the evolution of language. In (J. Trabant, Ed.) *Essays on the Origin of Language*. Berlin: Mouton, pp. 149–175.

Dunbar, R. (1996). *Grooming, Gossip and the Evolution of Language*. Cambridge, MA: Harvard University Press.

Durham, W. H. (1991). *Coevolution: Genes, Culture, and Human Diversity*. Stanford: Stanford University Press.

Edmunds, M. (1974). *Defense in Animals*. Harlow, Essex: Longman .

Gumperz, J. J. & Levinson, S. C. (Eds.) (1996). *Rethinking Linguistic Relativity*. Cambridge: Cambridge University Press.

Hauser, M. D. (1997). *The Evolution of Communication*. Cambridge, MA: Bradford Book, MIT Press.

Heeschen, V. (2001). The narration "instinct." In (J. Trabant, Ed.) *Essays on the Origin of Language*. Berlin: Mouton, pp. 179–196.

Henrich, J. & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior* **19**, 215–241.

Hinton, G. E. & Nowlan, S. J. (1987). How learning can guide evolution. *Complex Systems* **1**, 495–502.

Humphrey, N. (1999). Cave art, autism and the evolution of the human mind. *Journal of Consciousness Studies* **6**, 116–143.

Jablonka, E. & Rechav, G. (1996). The evolution of language in light of the evolution of literacy. In (J. Trabant, Ed.) *Origins of Language*. Workshop Series 2. Budapest: Collegium Budapest, pp. 70–88.

Jackendoff, R. (1999). Possible stages in the evolution of the language capacity. *Trends in Cognitive Sciences* **3**, 272–279.

Kirby, S. (2000). Syntax without natural selection: How compositionality emerges from vocabulary in a population of learners. In (C. Knight, J. R. Hurford & M. Studdert-Kennedy, Eds.) *The Evolutionary Emergence of Language: Social Function and Linguistic Form*. Cambridge: Cambridge University Press, pp. 303–323.

Knight, C. (1998). Ritual/speech coevolution: A solution to the problem of deception. In (J. R. Hurford, M. Studdert-Kennedy & C. Knight, Eds.) *Approaches to the Evolution of Language*. Cambridge: Cambridge University Press, pp. 68–91.

Kruuk, H. (1972). *The Spotted Hyena*. Chicago: University of Chicago Press.

Lewontin, R. (1978). Adaptation. *Scientific American* **239**, 157–169.

Lieberman, P. (1991). *Uniquely Human: The Evolution of Speech, Thought and Selfless Behavior*. Cambridge, MA: Harvard University Press.

Miller, G. F. (2000). *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature.* New York: Doubleday.

Odling-Smee, F. J., Laland, K. N. & Feldman, M.W. (1996) Niche construction. *American Naturalist* **147**, 641–648.

Ohnuma, K., Aoki, K. & Akazawa, T. (1997). Transmission of tool-making through verbal and non-verbal communication: Preliminary experiments in Levallois flake production. *Anthropological Science* **105**, 159–168.

Rappaport, R. A. (1999). *Ritual and Religion in the Making of Humanity.* Cambridge: Cambridge University Press.

Rasa, A. (1985). *Mongoose Watch: A Family Observed*. London: John Murray.

Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences* **24**, 309–382.

Savage-Rumbaugh, E. S. & Lewin, R. (1994). *Kanzi: The Ape at the Brink of the Human Mind*. New York: John Wiley.

Savage-Raumbaugh, S., Shanker, S. G. & Taylor, T. J. (1998). *Apes, Language and the Human Mind*. New York: Oxford University Press.

Sperber, D. (1996). *Explaining Culture: A Naturalistic Approach*. Oxford: Blackwell.

Sperber, D. & Wilson, D. (1986). *Relevance: Communication and Cognition*. Oxford: Blackwell.

Sober, E. & Wilson, D. S. (1998). *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.

Waddington, C. H. (1953). Genetic assimilation of an acquired character. *Evolution* **7**, 118–126.

Weber, B. & Depew, D. (Eds.) (2003). *Evolution and Learning: The Baldwin Effect Reconsidered*. Cambridge, MA: MIT Press.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour* **138**, 1489–1525.

Chapter IX

Climate Variability in the Levant and Northeast Africa during the Late Quaternary Based on Marine and Land Records

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Abstract

The Levant and northeast Africa are influenced by two different climatic systems. One originates in the northeast Atlantic Ocean, passing over Europe and the Mediterranean Sea. The other is the African/west Asian monsoonal system that originates in the low latitudes of the Atlantic or the Indian Ocean. In order to understand the long-range climate variability of these systems in the region, we compared well-dated marine and terrestrial records that cover several glacial-interglacial cycles. The land record is based upon the isotopic composition of cave deposits (speleothems) from the eastern Mediterranean and the marine record is based mainly upon the isotopic composition of planktonic foraminifera from the Mediterranean Sea, the Red Sea, and the Gulf of Aden. These records indicate that both systems, regulated by the orbital driven maximum summer insolation cyclicity, covary with each other and show a high degree of correspondence in their climatic variability. Extremely humid and rainy climate occurred over the entire region during warm interglacial intervals, when the Mediterranean frontal and the monsoonal systems became more intense and widespread and nearly overlapped. On the other hand, during glacial maxima, and during periods equivalent to Heinrich events, the entire region became extremely cool and dry. In between these extremes, dry and warm interglacial periods of broad extent, as well as cool and more humid glacial intervals of local to more regional extent, prevailed in the region.

Introduction

Climate change is thought to have driven hominid evolution (deMenocal 1995) and especially the "out-of-Africa" dispersal of hominids (Straus & Bar-Yosef 2001). One of the main routes of human dispersal out of Africa was the eastern route through NE Africa and the Levant. Our knowledge of climate variability in this region during the Quaternary is incomplete, mainly because the land records in the subtropical Sahara and Arabian deserts are few, scattered, of short duration, and difficult to date accurately. Tracing climate variability in this region is crucial for understanding the environmental settings that accompanied human dispersals out of Africa during the last ~2 Ma, including the ~125–100 Ka BP migration of *Homo sapiens* (Walter et al. 2000; Meignen et al. 2001). It is also important for understanding the ~60–10 Ka BP changes in hominid culture during the Middle-to-Upper Paleolithic transition and the subsequent Epipaleolithic (Bar-Matthews & Ayalon 2003).

With the initiation of glaciation in the Northern Hemisphere ~2.6 Ma ago (Ruddiman & Raymo 1988; Clemens et al. 1996), the earth witnessed frequent and large-scale oscillations between glacial (G) and interglacial (I) conditions. Changes in the earth's orbital geometry have been suggested to be the main cause of the succession of ice ages during this period (Imbrie et al. 1993). Between 2.6 Ma and ~1.0 Ma the climatic variations concentrated mainly at the 41 Ka cycles of orbital obliquity. Shifts towards 100 Ka cycles of orbital eccentricity started 1.2 Ma ago and become of large amplitudes during the last ~600

Ka. Coinciding with the onset of Northern Hemisphere glacial cycles ~2.6 Ma ago, the climate in the subtropics of Africa shifted toward more arid conditions (deMenocal 1995). The change into more dry and open conditions continued with two further steps at ~1.7 Ma and at ~1.0 Ma, turning the subtropics of Africa, as well as Arabia, into one of the most arid deserts on earth.

In addition to the general trend toward increasing aridity during the last ~2.8 Ma, as suggested by deMenocal (1995), the climate in this region has shifted between dry or more humid intervals following the global glacial and interglacial periodicity. The dry periods are associated with expansion of dry lands and increased eolian dust from the Sahara and Arabian deserts. On land, the more humid periods are associated with higher rainfall, greater riverine discharge, reduction in the size of the desert belt, and an increase in vegetation cover. In the marine records the water column may have become stratified and, in its deeper parts, dark, organic-rich sapropel layers may have accumulated.

In order to better understand the climate variability in NE Africa and the Levant during the Upper Quaternary, we integrate records shown in Figure 1 from the SE Mediterranean Sea (Fontugne & Calvert 1992; Rohling & de Rijk 1999; Emeis et al. 2000; Kallel et al. 2000; Almogi-Labin et al. 2001; Calvert & Fontugne 2001; Rohling et al. 2002a), the central Red Sea (Almogi-Labin et al. 1991, 1998; Hemleben et al. 1996; Rohling et al. 1998), and the Gulf of Aden (Almogi-Labin et al. 2000), and complement these marine records with land records from cave deposits in the Levant (Bar-Matthews et al. 1997, 1999, 2003; Frumkin et al. 1999). The advantage of using these records is that they are continuous, well dated, and undisturbed, and therefore easy to compare.

In this integration we attempt to compare the Mediterranean climate system, linked to the high-latitude NE Atlantic Ocean, with the African and west Asian monsoonal systems of low to mid-latitudes and determine how these systems interacted during the Upper Quaternary.

Regional climatic settings

Today, NE Africa, including the adjacent Red Sea and the Southern Levant, are parts of the vast Sahara-Arabian desert belt, with a climate that is characterized by little rain and a large daily temperature range. Farther to the north the conditions gradually become less extreme, turning into a Mediterranean climate in the Levant region. The entire region is influenced by two different climatic systems. One originates in the NE Atlantic Ocean, passing over Europe and the Mediterranean Sea (Rindsberger et al. 1983; Eshel 2002), and the second one originates in the tropical Atlantic or the southern Indian Ocean, passing over NE Africa or the southern Red Sea, and is associated with the low-latitude monsoonal system (cf. Rossignol-Strick 1985).

The SE Mediterranean climate is characterized by hot and dry summers between May and August, caused by sinking air of the subtropical highs. A strong high-pressure ridge pushes eastwards from the Azores subtropical high and develops over the Mediterranean. The Persian trough extends NW from the Persian Gulf and is associated with the west Asian (Indian) summer monsoon.

Winter in the SE Mediterranean region is cool and rainy, with rainfall from November to March-April with cyclonic disturbances and low mean pressure. The most developed eastern Mediterranean depression system is the "Cyprus low" that predominates during winter and early spring and has preferred tracks to the east or northeast.

The west Asian summer monsoon, also known as the SW monsoon, is driven by atmospheric pressure differences between land and ocean and is characterized by intense solar heating that leads to high temperatures over the Asian landmass (Clemens et al. 1991, 1996, and references therein). As hot air expands and rises, a semi-permanent low-pressure area develops. This causes an inter-hemispheric transport of heat and moisture from the Atlantic through Africa and from the southern Indian Ocean through the northern Arabian Sea toward central Asia.

The monsoon wind directions reverse biannually and the SW monsoon system is replaced by the NE monsoon system. This reversal is due to temperature differences

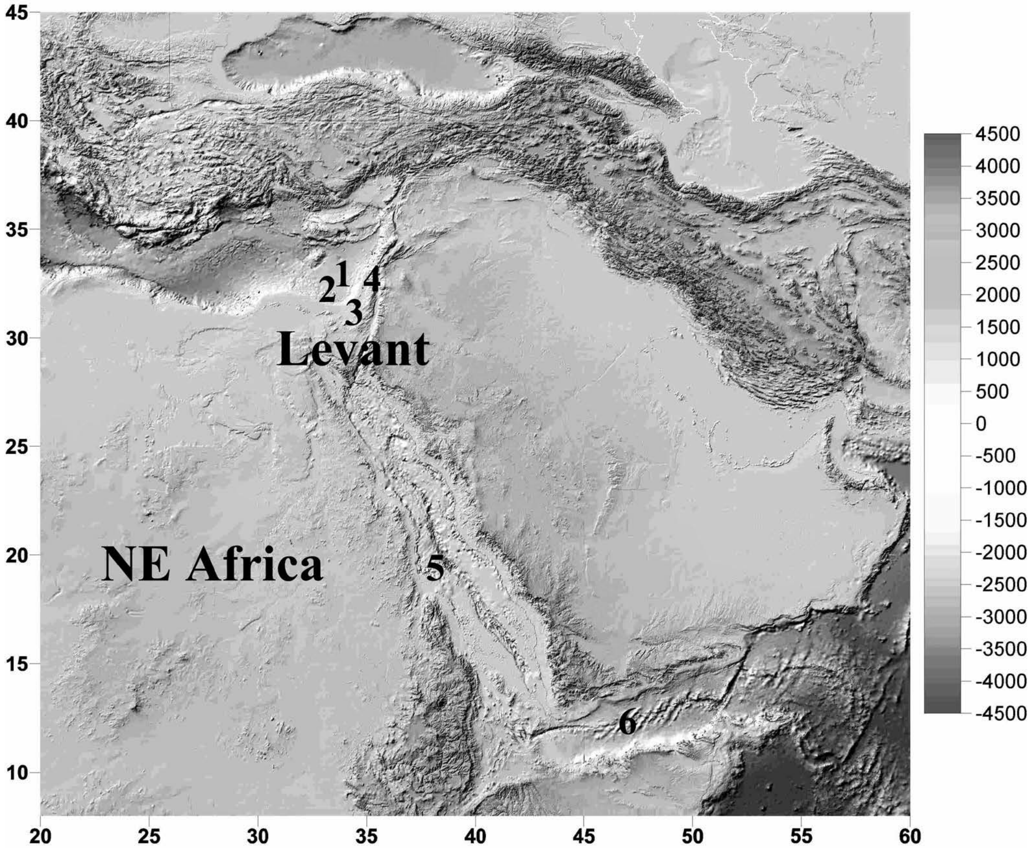

Figure 1. Location map showing the six sites in the SE Mediterranean Sea, the Levant, the Red Sea, and the Gulf of Aden from which the records were taken for the paleoclimate synthesis: 1) Core MD 84 641, 33°02′N, 33°38′E, 1375 m water depth (Fontugne & Calvert 1992; Calvert & Fontugne 2001); 2) Core MD 84 642, 32°40.9′N, 32°34.9′E, 1260 m water depth (Cheddadi & Rossignol-Strick 1995); 3) Soreq Cave, 31°45′N, 35°03′E, 40 km inland, ~400 m above sea level (Bar-Matthews et al. 1997, 1999, 2003); 4) Peqiin Cave, 32°58′N, 35°19′E, 25 km inland, ~650 m above sea level (Bar-Matthews et al. 2003); 5) Core M5/2-174/87-2, KL 11, 18°46.3′N, 39°19.9′E, 825 m water depth from the Red Sea (Hemleben et al. 1996; Almogi-Labin et al. 1991, 1998); 6) The Gulf of Aden, core M5/2-259/87-2, KL15, 12°51.5′N, 47°25.9′E, 1631 m water depth (Almogi-Labin et al. 2000). The map is based upon the 0.5′ digital terrain model prepared by Dr. John K. Hall (GSI) for the General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas.

between land and ocean between December and February, when the continental landmass cools, rapidly resulting in extremely low temperatures over central Asia. As temperatures drop, atmospheric pressure rises and an intense high-pressure system, also known as the Siberian high, develops with NE winds.

The Levant, northern Red Sea, Gulf of Suez, and Gulf of Aqaba are influenced mainly by the Mediterranean depression systems. The southern parts of the Red Sea, as well as parts of NE Africa, are influenced by the winter and summer low-latitude monsoonal systems.

Paleoclimate proxies

The oxygen isotopic record ($\delta^{18}O$) of the surface-dwelling planktonic foraminifera *Globigerinoides ruber* is used for paleoclimate reconstruction. Their $\delta^{18}O$ values record changes in shell precipitation temperature of the ambient seawater and in $\delta^{18}O$ of the seawater, thus reflecting changes in sea surface temperature and ice volume. In addition, the $\delta^{18}O$ composition of the foraminifera provides a basis for developing a geological time-scale (Imbrie et al. 1984). In this study, we correlate the $\delta^{18}O$ records of *G. ruber* from the studied sites with the global chronology known as the SPECMAP standard record, enabling us to date the $\delta^{18}O$ records of *G. ruber*.

Sediment properties such as total organic carbon and sediment color index (Fontugne & Calvert 1992; Emeis et al. 2000) are used as indicators of the periodic accumulation of dark, organic-rich sapropel layers in the eastern Mediterranean Sea. Element ratios of Ti/Al, Si/Al and K/Al preserved in sedimentary records from the deep eastern Mediterranean Sea were used as tracers of climate variability on land (cf. Wehausen & Brumsack 1999). These authors suggest that high values of these element ratios deriving from palygorskite, kaolinite, and illite coincide with relatively dry periods of increased eolian dust originating from the Sahara desert. During wet periods these ratios become low because of high riverine discharge, mainly of the Nile River, with dominant smectite and chlorite.

Another proxy that is used for tracing climate variability in the Red Sea area is the high sensitivity of pteropods, which are holoplanktonic gastropods, to water column oxygenating conditions. Their sensitivity is expressed by large variations in abundance of surface (epipelagic/non-migratory) and intermediate water (mesopelagic/migratory) pteropods (Almogi-Labin et al. 1991, 1998). During periods of a more stratified water column and well-developed oxygen minimum zone (OMZ), the assemblage is dominated by epipelagic pteropods. When the intermediate water column becomes moderately to well aerated, similar to present-day conditions, mesopelagic pteropods are the dominant species (Weikert 1982; Almogi-Labin 1984; Auras-Schudnagies et al. 1989). The degree of stratification of the water column depends on the regional climate. More humid periods in the northern and central parts of the Red Sea are associated with an expanded OMZ and a strongly stratified water column, and hence predominance of epipelagic pteropods. During increasingly dry intervals, the water column became well aerated and mesopelagic pteropods became dominant.

Well-dated land records are based on cave deposits (speleothems; Kaufman et al. 1998; Bar-Matthews et al. 2003). Their $\delta^{18}O$ values record average annual temperatures, variations in rainfall amount, and the origin of storm tracks (i.e., the severity of winters).

Integrating all the above-mentioned proxies from the marine records, as well as the continental records, enables us to reconstruct the general paleoclimate variability in the Levant and NE Africa and define the boundary conditions in which the climatic system was acting as the region's climate became increasingly arid (e.g., deMenocal 1995). We first describe the climate variability of the humid interglacial stages based on the eastern Mediterranean marine records, the Levant land records, and the marine records of the Red Sea. We describe the dry spells of interglacial stages later on. We then discuss the glacial stages, first considering the arid periods and then turning to the more humid glacial intervals.

Humid conditions during warm interglacial stages

The deep-sea sedimentary record of the eastern Mediterranean Sea is composed of alternating light and dark sediments that show a distinct cyclicity (Olausson 1961; Vergnaud-Grazzini et al. 1977; Fontugne & Clavert 1992; Emeis & Sakamoto 1998). The dark, organic carbon-rich sapropel layers predominantly occur during interglacial stages with a few exceptions of some glacial sapropels (Rossignol-Strick 1985; Rossignol-Strick et al. 1998). The sapropels are generally finely laminated, devoid of benthic fauna, and rich in sulfides indicating accumulation in anoxic conditions. The accumulation of dark organic-rich sapropels contrasts with recent light-colored sediments that accumulate in highly oxygenated bottom water with oxygen concentrations of 3–4 ml O_2/l (Klein et al. 1999). The development of anoxic conditions is restricted to the deeper parts of the eastern Mediterranean Sea (cf. Emeis and Sakamoto 1998) and seems to result from the cessation of deepwater formation due to strong intermediate to surface water stratification (Rohling & Giesks 1989; Jorissen 1999). The sapropel layers (Figure 2a) are associated with low foraminiferal $\delta^{18}O$ values, often below -1‰. Emeis et al. (2000) have suggested that these low values result from the combined effect of sea-surface temperature rise and mainly the enhanced supply of fresh water from the eastern Mediterranean borderland (Kallel et al. 1997; Rohling et al. 2002a). This is also evident from the distinct minima in Ti/Al, Si/Al and K/Al within all sapropels, which are indicative of high riverine supply mainly from the Nile River (cf. Wehausen & Brumsack 1999; Calvert & Fontugne 2001). The high Nile River discharge during sapropel events is caused by intensification of the African monsoon at the headwaters of the White Nile in eastern equatorial Africa and in the Ethiopian Highlands where the Blue Nile and the Atbara originate.

All sapropel events coincide with astronomically driven maximum summer insolation at 65N latitude and maxima in radiation at the 19–23 Ka cycles of orbital precession. The link between sapropel events and astronomical "Milankovitch" cycles goes back to the early-middle Pleistocene (cf. Rossignol-Strick 1983; Rossignol-Strick et al. 1998). Because of their regular occurrence, sapropels have been used for establishing a refined time-scale calibration for the entire Pliocene (Lournes et al. 1996; Emeis & Sakamoto 1998). The direct link between sapropels and more humid climatic conditions in NE Africa and the Levant goes back from the Recent to the early Pliocene, indicating the constancy of this system.

On land, speleothem records from the Soreq and Peqiin Caves (Bar-Matthews et al. 2000, 2003) show recurring intervals of exceptionally low $\delta^{18}O$ values of -8.4‰, compared to the present-day average value of -5.4±0.2‰ (Figure 2b). The anomalously low $\delta^{18}O$ values have been attributed to an increase in rainfall of ~40–50% compared to the present-day average precipitation of 500–550 mm y^{-1} in the vicinity of the Soreq Cave. The above-average rainy intervals recognized in the Levant, of ~3–6 Ka duration, coincide with the periodic accumulation of sapropels in the eastern Mediterranean Sea (Bar-Matthews et al. 2000, 2003; Ayalon et al. 2002). They also coincide with some other land records from NE Africa and the SE Mediterranean region that indicate a warm humid climate in this region during the early Holocene and during the penultimate interglacial marine isotope stage (MIS) 5.5 (Street & Grove 1976; Ritchie et al. 1985; COHMAP Members 1988; Haynes et al. 1989; McKenzie 1993; Gasse & van Campo 1994; Rossignol-Strick 1999; Rohling et al. 2002a). During humid interglacial intervals the calcite speleothems are composed of small-sized, randomly oriented crystals, rich in detrital material. Their trace element concentrations of Sr, Ba, and U, and the ratios of $^{87}Sr/^{86}Sr$ and $^{234}U/^{238}U$, reach minimum values (Figure 3). Their petrography, as well as their chemical and isotopic composition, are indicative of their formation from fast-flowing water, resulting in a large input of detritus and oxides and a larger input of the dolomitic host rock due to enhanced weathering as a result of increased rainfall conditions (Kaufman et al. 1998; Ayalon et al. 1999).

All of these records, the terrestrial and the marine ones, indicate a simultaneous increase in rainfall over NE Africa and the Levant, at least during the early Holocene and during the penultimate MIS 5.5, turning the entire region into a relatively more humid zone. The retreat of the Sahara desert to a minimum during these humid intervals seems also to be reflected by the lower element ratios of Ti/Al, Si/Al and K/Al (Calvert & Fontugne 2001). The Mediterranean fronts probably penetrated farther south over NE Africa, beyond their present-day track (Arz et al. 2003a), while the African monsoonal system shifted to its maximal northern position (cf. Haynes et al. 1987; Street-Perrott & Perrott 1993; Rohling et al. 2002a). The simultaneous occurrence of humid climate conditions in areas influenced by the low-latitude African monsoonal system together with areas affected by the high-latitude NE Atlantic system (e.g., the Levant cave deposits and the northern parts of the Sahara desert) suggest a common cause (at least in its broader sense). It may be that maximal summer insolation in the Northern Hemisphere, which is controlled by earth orbital geometry, simultaneously modulated both systems.

The deep Red Sea sedimentary record is devoid of any sapropels except the dark layers that accumulated during the Deglaciation between 14.6–13.2 and 11–10.4 Ka BP (Almogi-Labin et al. 1991, 1998; Hemleben et al. 1996; Arz et al. 2003b). The absence of sapropel layers in the Red Sea

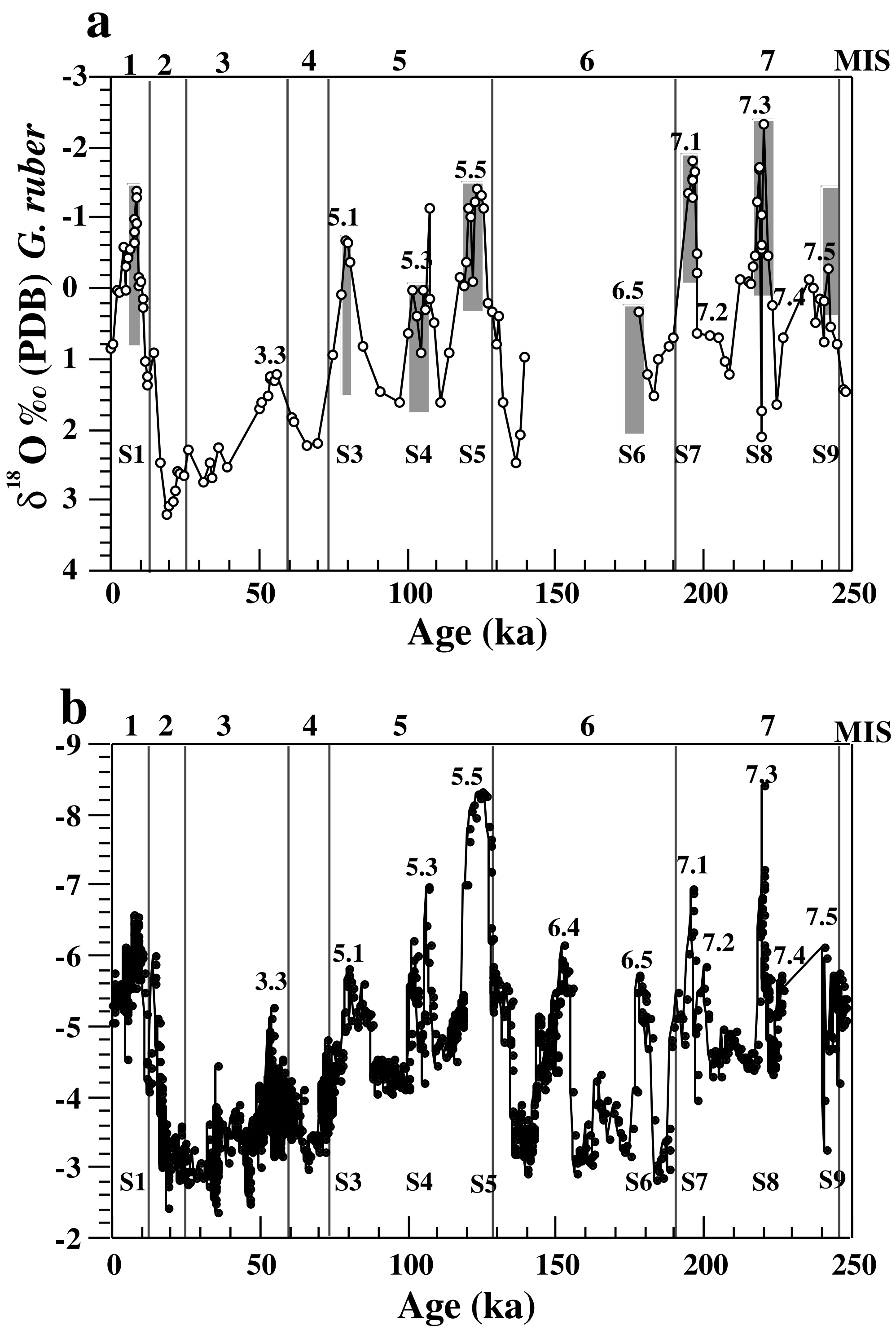

Figure 2. Comparison between the δ^{18}O record of *Globigerinoides ruber* (a) from core MD 84 641 (modified after Fontugne & Calvert 1992) and the oxygen isotope record (b) of Soreq Cave speleothems for the time period of 185 Ka to the present day and Peqiin Cave speleothems from 250 to 185 Ka. The marine record was adjusted to the speleothem age record in three intervals (see Bar-Matthews et al. 2003 for details). Seven marine isotope stages (MIS 1–7) are marked and divided by vertical bars. The substages are also marked. The gray areas indicate sapropel horizons (S1–S9) in core MD 84 641 from the SE Mediterranean Sea.

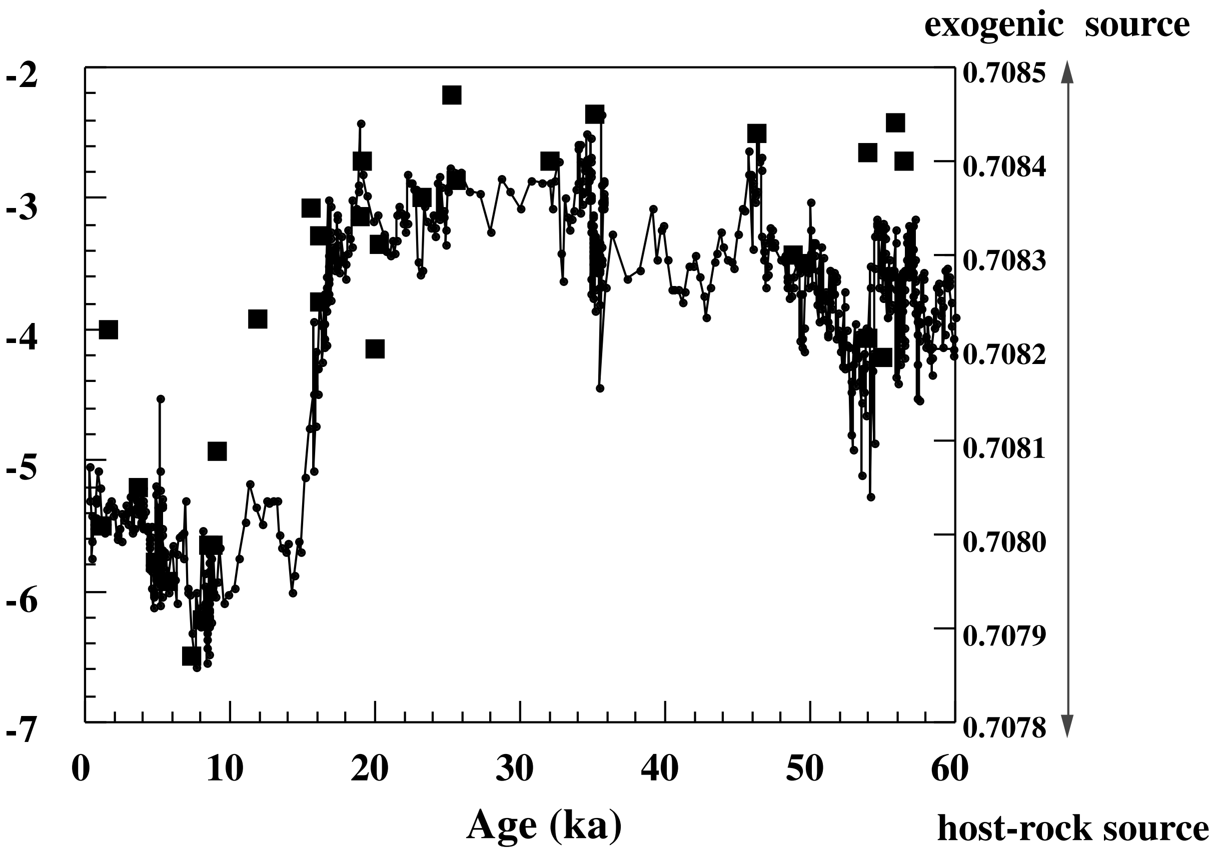

Figure 3. $^{87}Sr/^{86}Sr$ ratios of Soreq Cave speleothems (black squares) superimposed on $\delta^{18}O$ profile against age for the last 60 Ka (from Ayalon et al. 1999). The high $^{87}Sr/^{86}Sr$ values reflect exogenic sources (dust and marine spray); the lower values are closer to the Upper Cretaceous dolomitic host rock value of 0.7074.

that borders NE Africa and the Southern Levant is probably connected to the fact that it is an elongated landlocked basin surrounded by mountains, with a relatively small drainage system and no large rivers flowing into it. Moreover, much of the Red Sea water column structure is regulated by climate change over the northernmost Red Sea and the shallow-water Gulf of Suez (Cember 1988; Eshel et al. 1994; Woelk & Quadfasel 1996). Because the northernmost part of the Red Sea lies in the heart of the subtropical Sahara-Arabian desert belt, it is the area least influenced by the predominating African monsoon or the Mediterranean climate system. Nevertheless, based on the increase in the relative abundance of epipelagic vs. mesopelagic pteropods, it was suggested by Almogi-Labin et al. (1998) that more humid conditions prevailed in the surroundings of the northern and central parts of the Red Sea during certain interglacial intervals (Figure 4). Most of these intervals correspond to humid periods recognized in NE Africa and the Levant. Among them are the humid intervals of interglacial MIS 5.3, 5.5, 7.1, 7.3, 7.5 and to a lesser degree 11.1, corresponding to sapropels S4, S5, S7, S8, S9 and S11, respectively. One of the most prominent humid phases in the region, corresponding to sapropel S1 of the early Holocene, is hardly detected by this criterion, namely the relative abundance of epipelagic pteropods, in the Red Sea record (Almogi-Labin et al. 1998). Moreover, there are no records for sapropel S10 of MIS 9, because of the lack of pteropods due to their poor preservation during this interval.

The duration of the more humid intervals observed in the Red Sea records seems to be shorter in comparison to

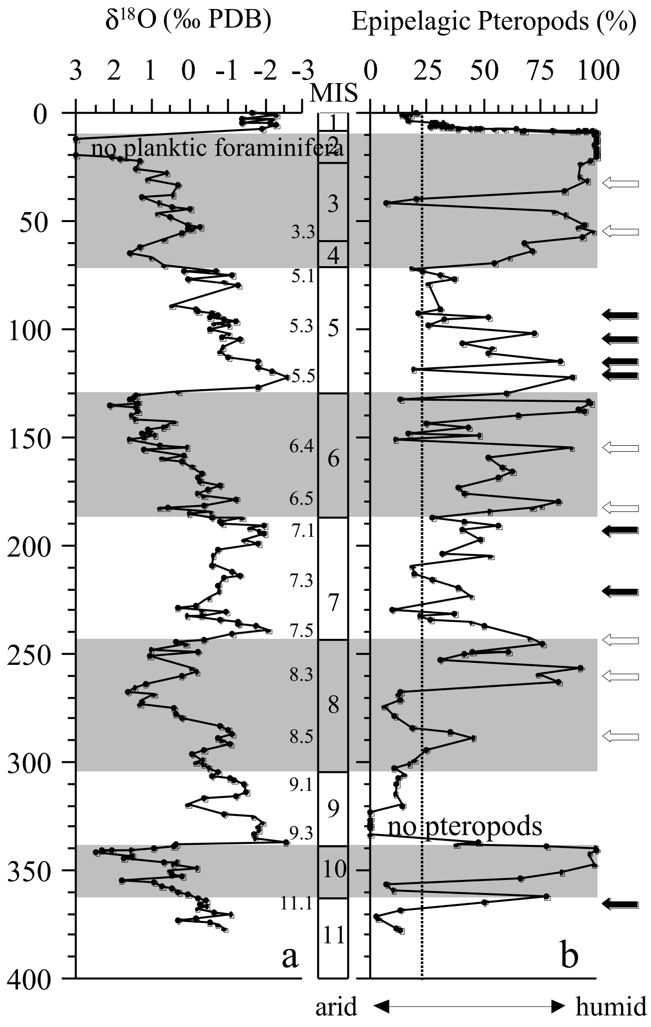

Figure 4. The δ¹⁸O record of *Globigerinoides ruber* (a) of core M5/2-174/87-2, KL 11 (Hemleben et al. 1996), central Red Sea, during the last 380 Ka. Numbers on the right side of the stable isotope record indicate marine isotope stages (MIS) and substages, and the relative abundance of epipelagic (b) pteropods (modified after Almogi-Labin et al. 1998). The vertical dashed line indicates the % epipelagic pteropods at present. Solid arrows represent periods with more humid conditions during interglacial intervals and open arrows indicate periods of more humid conditions during glacial stages. The shaded areas indicate glacial intervals.

Mediterranean marine sapropel events, and especially compared with the more humid periods represented by the speleothem records. This might reflect differences in the time-response of marine vs. land systems to climate change (the response of the biogenic proxy, e.g., pteropods). It may also be due to the generally steep N-S gradient of Mediterranean climate fronts and the S-N gradient of the African monsoonal system, due to the periodic northward shift of the Inter Tropical Convergence Zone.

Dry intervals during warm interglacial stages

During the interglacial substages, in between the sapropel events (e.g., MIS 5.2, 5.4, 7.2, 7.4, etc.), the $\delta^{18}O$ values of foraminifera are 1–2‰ higher than their values during the sapropel intervals (Figure 2a). High-resolution studies in the eastern Mediterranean marine and land records indicate that the humid climate of the early Holocene was replaced at ~6–5 Ka BP by more arid conditions (Bar-Matthews et al. 1998). During the last 5–6 Ka the $\delta^{18}O$ values of foraminifera from the eastern Mediterranean marine records increased by 1–1.5‰ (Fontugne & Calvert 1992). The increase in $\delta^{18}O$ during the late Holocene, as well as during other non-sapropel interglacial intervals, is connected to the increasing aridity in this region, with evaporation considerably exceeding the amount of precipitation. A coeval increase in the $\delta^{18}O$ of the speleothem record (Figure 2b) was related to a considerable decrease in rainfall amount (Bar-Matthews et al. 1997, 1998, 2003). Moreover, the element ratios of Ti/Al, Si/Al, and K/Al are higher during the interglacial non-sapropel intervals, resembling the values of glacial periods. The higher element ratios indicate a shift in the source of the terrigenous material from a fluvial Nilotic to an eolian source (cf. Wehausen & Brumsack 1999; Calvert & Fontugne 2001). The increase in dust supply follows the retreat south of the African monsoonal system from its maximal position during the early Holocene (Haynes 1987; Rohling et al. 2002a). A possible coeval shift northward of the Mediterranean fronts track to its present-day position may have caused increasing aridity in NE Africa and the Levant and the expansion of the Sahara and Arabian deserts to their current dimensions.

In addition to the general Holocene climate change from a humid early Holocene to a more arid late Holocene, several short-duration dry spells (on the order of a few decades to centuries) also occurred. The earliest one is the 8.2 Ka BP dry spell, first recognized in high-latitude records by Alley et al. (1997) and later found in the Levant cave deposits (Bar-Matthews et al. 1999), ice-core and lake records from NE Africa (Gasse & van Campo 1994; Thompson et al. 2002), and also in eastern Mediterranean marine records (Rohling et al. 1997). Another dry spell, recently described by Rohling et al. (2002a) and possibly evident in the record described by Kallel et al. (2000), is similar in nature to the 8.2 Ka BP event, interrupting the penultimate interglacial humid period. Rohling et al. (2002a) noticed that this event was short and occurred in the middle part of the S5 sapropel event, and thus concluded that its age is approximately 122 Ka BP. The 8.2 and the 122 Ka BP dry spell events are connected to the periodic strengthening of higher latitude circulation and the temporary withdrawal of the monsoonal system to lower latitudes. Additional dry spells during the Holocene occurred in the Levant at ~5.1 and ~4 Ka BP (Bar-Matthews et al. 1998, 2003).

In the Red Sea there is also clear evidence of a trend toward increasing aridity during a period lasting ~1000 y, starting at ~5.2 Ka BP and culminating at ~4.2 Ka BP. This aridity trend is evident from the increase in abundance of the pteropod *Limacina bulimoides*, an important climate indicator species (Figure 5). This mesopelagic/migratory species, which does not live today in the central and northern Red Sea, is indicative of an aerated intermediate water column (Weikert 1982; Almogi-Labin et al. 1984). *Limacina bulimoides* reached its maximum abundance at ~4.2 Ka BP, indicating a period of more vigorous intermediate water formation related to more arid conditions in the northern and central parts of the Red Sea (Almogi-Labin et al. 1991; Edelman-Furstenberg 1998) and in the Gulf of Aqaba (cf. Almogi-Labin 1982).

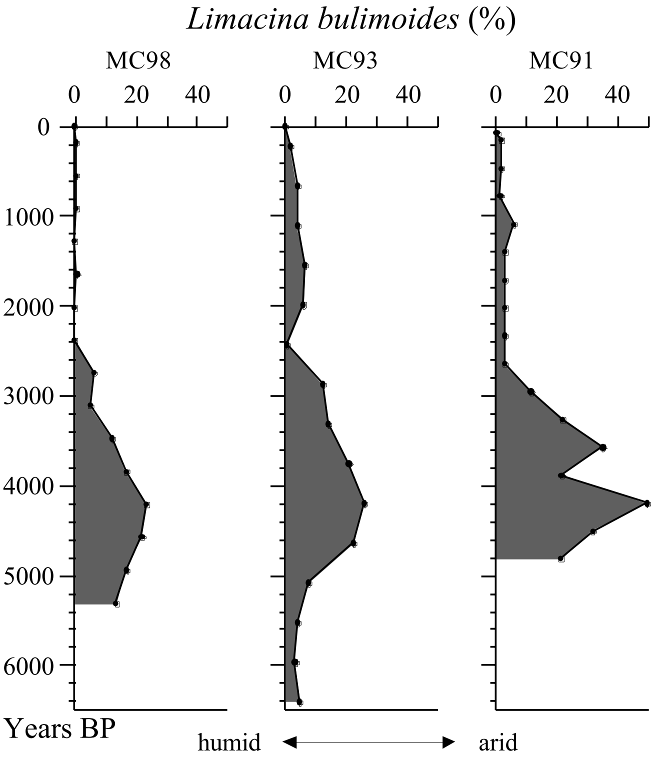

Figure 5. The relative abundance of *Limacina bulimoides*, a mesopelagic pteropod, out of the total pteropods during the late Holocene, from three multicores from the central Red Sea: MC98, 579 m water depth; MC93, 929 m water depth; and MC91, 1781 m water depth plotted against uncalibrated ^{14}C age (modified after Edelman-Furstenberg 1998).

The climate event marked by the ~4.2 Ka BP abundance peak of *Limacina bulimoides*, and coinciding with the exceptional dry spell recorded in the Soreq Cave (Bar-Matthews et al. 1998), is of a large regional scale. This event has been recorded in Egypt (Hassan & Stucki 1987; Hassan 1996) and Mesopotamia (Weiss et al. 1993) and has been viewed as causing the end of the Old Kingdom in Egypt and the collapse of the northern Mesopotamian civilization. Taken together, the evidence indicates that the increasing aridity at ~4.2 Ka BP affected a vast area including the Middle East as well as NE and eastern equatorial Africa (e.g., Thompson et al. 2002).

The use of *Limacina bulimoides* as an indicator of dryer periods compared with the present-day climate (Almogi-Labin et al. 1998) enables us to recognize several additional dry spells in the Red Sea during interglacial stages (Figure 6). Some were extremely short, such as the ~122 Ka BP dry spell, which is the equivalent of the dry

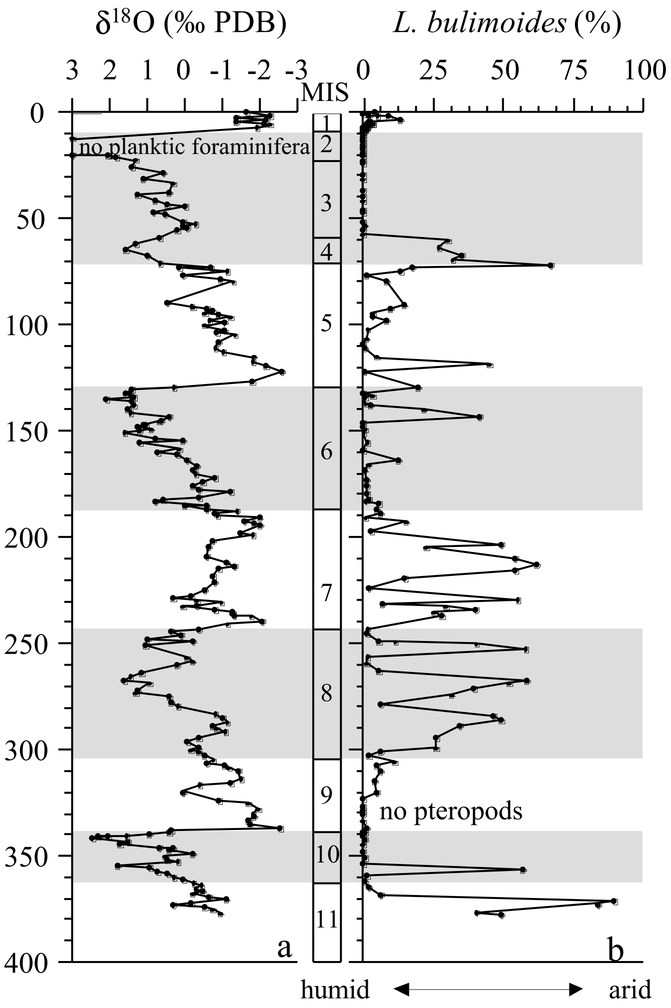

Figure 6. The $\delta^{18}O$ record of *Globigerinoides ruber* (a) of core M5/2-174/87-2, KL 11, central Red Sea, during the last 380 Ka (Hemleben et al. 1996). Numbers on the right side of the stable isotope record indicate marine isotope stages (MIS) and the relative abundance of the mesopelagic pteropod *Limacina bulimoides* (b) out of the total pteropods (modified after Almogi-Labin et al. 1998). The shaded areas indicate glacial intervals.

spell recorded by Rohling et al. (2002a) in the eastern Mediterranean Sea, and a short event at the top of MIS 11.2. Other dry events during interglacial periods that were probably more arid than the present-day climate were of longer duration, lasting ~5–10 Ka; these occur at ~210 Ka BP and ~230 Ka BP, coeval with interglacial MIS 7.2 and 7.4.

Dry periods during cool glacial stages

During glacial maximum intervals, and notably during the Last Glacial Maximum (LGM, ~23–18 Ka BP), the eastern Mediterranean Sea became a more concentrated basin with foraminiferal $\delta^{18}O$ values (Figure 2a) exceeding ~3.0‰ (Fontugne & Calvert 1992; Kroon et al. 1998; Rohling & De Rijk 1999, and reference therein). During the older glacial maximum intervals of MIS 6, 8, and 10, $\delta^{18}O$ values were slightly lower, varying between 2 and 2.5‰ (Figure 2a). Rohling and De Rijk (1999) pointed out that during the LGM a steep W-E water oxygen isotope gradient (δ_w) existed in the Mediterranean Sea, differing by roughly a factor of 3 from the present isotope gradient (0.9‰ in the west, 1.7‰ in the east). This gradient resulted mainly from the increasing $\delta^{18}O$ in the Levantine basin because of intensified evaporation. The increase in $\delta^{18}O$ also resulted from the fact that the two main conveyors of fresh water into the eastern Mediterranean Sea, the Black Sea and the Nile River, were nearly shut down. The Black Sea was entirely disconnected from the Mediterranean during the LGM because of the global sea-level drop, while the Nile River during this period was a braided, highly seasonal river that hardly supplied water to the eastern Mediterranean. This was mainly because of severe aridity at the headwaters of the Nile River tributaries and also in other parts of NE Africa (Adamson et al. 1980; Gasse 2000; Talbot et al. 2000).

Temperature estimates from the Levant, based on pollen records and regional model simulation, have suggested a temperature decrease of ~6°C below present-day average values during the LGM (e.g., Horowitz 1979; Cheddadi & Rossignol-Strick 1995; Ganopolski et al. 1998). Based on fluid inclusions in Israeli speleothems, Bar-Matthews et al. (1997) and Matthews et al. (2000) have suggested a temperature drop of ~8°C during the LGM. Pollen records from the SE Mediterranean Sea indicate severe aridity during the LGM and during the penultimate glacial maximum interval (Cheddadi & Rossignol-Strick 1995). Land records from the northern Negev desert, Israel, also indicate a drier climate with extensive erosion during the LGM (Goodfriend & Magaritz 1988). The suggestion that rainfall decreased during the LGM is based on the increase in $\delta^{18}O$ values in Israeli cave speleothems to ~-2.4‰ at 21–19 Ka BP compared to the present-day average $\delta^{18}O$ value of -5.4 ± 0.2‰ (Bar-Matthews et al. 2003; see Figure 2b). High speleothem $\delta^{18}O$ values, similar to the LGM values, also occurred during short spells coinciding with the high-latitude Heinrich events H1-H5 (Bond et al. 1993), indicating that during these events cold and drier conditions also prevailed in the Levant (Bar-Matthews et al. 1999). Additional evidence for aridity during the LGM, and during Heinrich events, comes from Lake Lisan, the precursor of the present Dead Sea that covered large parts of the Dead Sea basin during the last glacial period. Major drops in lake level occurred at ~16, ~24, ~30, ~38, and between 47 and 45 Ka BP, corresponding with Heinrich events H1–H5, respectively (Bartov et al. 2003). The immediate response of the local hydrologic system, as reflected independently by the speleothems and the Lake Lisan records, indicates that climate variability in the Levant region is directly transferred from high to mid-latitudes via the NE Atlantic climate system (cf. deMenocal et al. 2000; Eshel 2002; Rohling et al. 2002b), or, alternatively, directly from the Siberian high-pressure system that was more developed during this period (cf. Almogi-Labin et al. 2000).

The element ratios of Ti/Al, Si/Al, and K/Al, which are sensitive indicators of North African climate variability, were in general high during glacial stages, with some exceptionally high spikes during glacial maximum conditions (Almogi-Labin et al. 2001; Calvert & Fontugne 2001). The high element ratios result from increased eolian dust flux originating from the Sahara desert and indicating dry to hyper-arid climate in the northern subtropics of Africa.

As a result of the dry conditions, during glacial intervals the calcite speleothems are characterized by thick calcite lamina comprised of large, coarse-grained, light-colored crystals showing preferred orientation and containing less than 0.1% detrital material. The large calcite crystals must have formed from slowly dripping water probably reflecting relatively dry conditions. Trace element concentrations of Sr, Ba, and U, and maximum ratios of $^{87}Sr/^{86}Sr$ (Figure 3) and $^{234}U/^{238}U$, are indicative of higher proportions of exogenic sources, probably dust and sea-spray, relative to the contribution from the weathering of host rocks (Kaufman et al. 1998; Ayalon et al. 1999).

Dry climate during the LGM, as well as during other glacial maximum stages, is also suggested by $\delta^{18}O$ values of foraminifera from the Red Sea (Hemleben et al. 1996). The $\delta^{18}O$ record is characterized by large-scale G/I amplitudes of up to ~6‰ between MIS 2 and MIS 1, much higher than the ~1.2‰ attributed to the global oceanic ice volume effect (Fairbanks 1989). The $\delta^{18}O$ record of foraminifera from the Red Sea is similar during interglacials to the nearby record from the Gulf of Aden (Almogi-Labin et al. 2000), which is considered to represent the "global oceanic record" (Figure 7). This is because Red Sea surface water derives directly from the Gulf of Aden due to the anti-estuarine circulation pattern of the Red Sea. However, during glacial maxima there is a maximal difference between the two $\delta^{18}O$ foraminiferal records because of the increasing isolation of the Red Sea following sea-level drop and climate change.

The LGM, and probably also the glacial maximum of MIS 6 and 12 (~20, ~135, and ~450 Ka BP, respectively), were the most extreme dry periods during the last 0.5 Ma, with a ~50% increase in sea surface salinity, making the Red Sea temporarily hostile to planktonic foraminifera and to most holoplanktonic pteropods, which disappeared during these intervals (Reiss et al. 1980; Almogi-Labin 1982; Hemleben et al. 1996; Almogi-Labin et al. 1998; Rohling et al. 1998; Fenton et al. 2000). In addition, authigenic aragonite was precipitated on the seafloor during the LGM because of the hypersaline conditions (Degens & Ross 1969; Milliman et al. 1969; Almogi-Labin et al. 1986; Arz et al. 2003b). A significant salt buildup occurred in the Red Sea during glacial maximum conditions, and especially during the LGM, reflecting the extremely arid conditions that prevailed in the Red Sea region (Gasse 1977; Adamson et al. 1980).

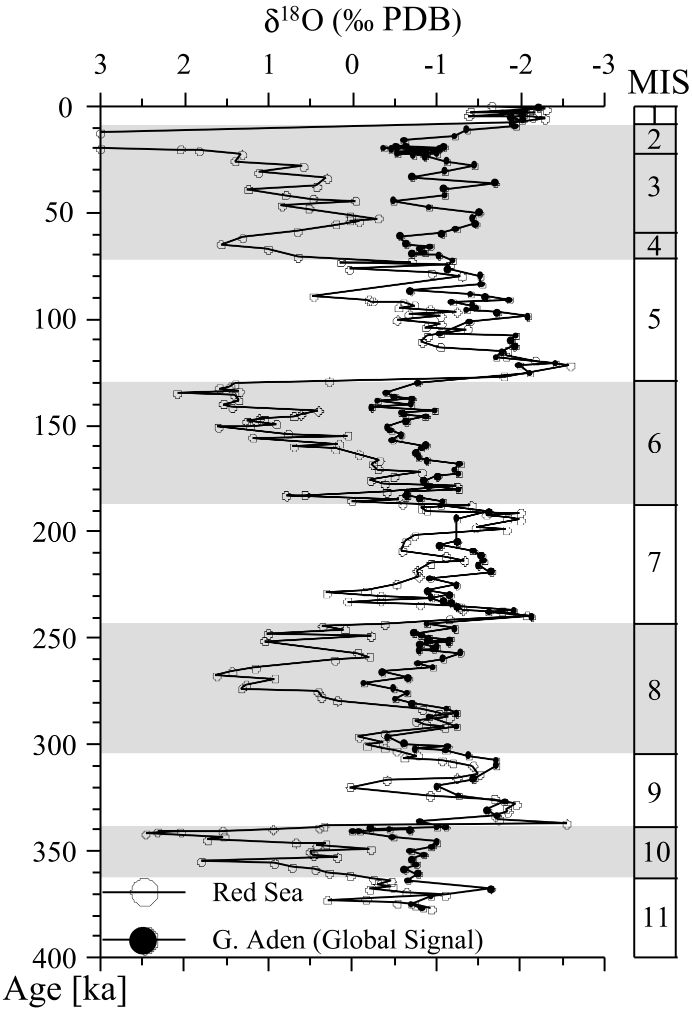

Figure 7. The $\delta^{18}O$ record of *Globigerinoides ruber* of core M5/2-174/87-2, KL 11 (open circles), central Red Sea (Hemleben et al. 1996), superimposed on the $\delta^{18}O$ values of *G. ruber* of core M5/2-259/87-2, KL15 (solid circles), Gulf of Aden (Almogi-Labin et al. 2000), showing similarity between the isotopic trends. Numbers on the right side of the oxygen isotope record indicate marine isotope stages (MIS). The shaded areas indicate glacial intervals.

Relatively humid periods during cool glacial stages

The climate in the Levant during MIS 3 and MIS 6 was cooler, with a decrease in rainfall amount relative to the present-day average (Cheddadi & Rossignol-Strick 1995). However, during discrete short intervals within these glacial stages, there is isotopic evidence from the Soreq Cave speleothems of sharp increases in rainfall (Figure 2b). This is reflected by decreases in $\delta^{18}O$ values during short events at ~36 and ~44, and longer, 2–5 Ka duration events at ~55, 152, and 178 Ka BP (Bar-Matthews et al. 1999; Ayalon et al. 2002). Coinciding with the low $\delta^{18}O$ values, ^{13}C values are also low (~-11 to -12‰), pointing to the dominance of C-3 type vegetation. Lake Lisan records indicate that during large parts of MIS 3 the lake level was ~100 m above the late Holocene level and that it was stable around 280–290 m below mean sea level (msl). The lake reached its highest level of ~165 m below msl only at the end of MIS 3, at 26–25 Ka BP (Bartov et al. 2003). The sharp increase in lake level at the end of MIS 3, indicative of cooler pluvial conditions, agrees with other records from the region, such as the gradual increase in $\delta^{18}O$ values (on the order of 1.5‰) recorded in foraminifera from the SE Mediterranean Sea between MIS 3.3 and the end of MIS 3 (Figure 2a, and Fontugne & Calvert 1992). Pollen records point to a short period of enhanced pluvial activity during this interval (Cheddadi & Rossignol-Strick 1995), paleosols developed in the northern Negev desert (Goodfriend & Magaritz 1988), and intensive speleothem formation occurred in the "rain shadow" desert of the Jordan Valley (Vaks et al. 2003).

In the Red Sea there are also indications of mild and relatively more humid climate conditions during large parts of MIS 3. Epipelagic pteropods dominate the assemblage between ~60 and ~47 Ka BP and between ~38 and ~25 Ka BP (Figure 4, and Almogi-Labin et al. 1986, 1998; cf. Reiss et al. 1980). Their dominance indicates that the water column was highly stratified with a well-developed OMZ related to a milder climate in the northern Red Sea. Another line of evidence for milder climate in the Red Sea region comes from the stable isotope record of foraminifera from the northern and central parts of the Red Sea. The small difference in $\delta^{18}O$ values (less than 1‰) between these records at 30 to 25 Ka BP (Geislhart 1998) indicates that the S-N salinity gradient had diminished considerably.

Epipelagic pteropods comprise the majority of the assemblage during other relatively humid glacial intervals as well, i.e., MIS 6.3 and 6.5, ~155 and ~180 Ka BP, respectively, and during MIS 8.3 and 8.5, at ~260 and ~290 Ka BP, respectively.

Summary

Climate variability in NE Africa and the Levant has been quite considerable during the last 400,000 years, affecting human evolution and the timing of the out-of-Africa dispersal of hominids. The climate in this region is regulated by the interplay between the high-latitude NE Atlantic/Mediterranean frontal system and the low-latitude African/west Asian monsoonal systems.

The most humid/rainy periods occur regularly during warm interglacial stages associated with enhanced relative to present-day rainfall on land in the Levant. They also correspond to deep eastern Mediterranean Sea sapropel events, high Nile River discharge, and a highly stratified water column in the Red Sea. The humid/rainy intervals coincide with maximum summer insolation at 65°N and maximum in radiation at the 19–23 Ka cycles of orbital precession. During humid/rainy intervals the maximal southward shift of the high-latitude NE Atlantic/ Mediterranean frontal system and the maximal northward shift of the low-latitude African/west Asian monsoonal systems (i.e., the Inter Tropical Convergence Zone) resulted in expansion of the vegetation cover in the present-day dry and barren areas of the Sahara and Arabian deserts. The most humid/rainy intervals during the last 400,000 years occurred at ~9, ~105, ~125, ~200, ~220, ~240, ~305, ~335, and ~365 Ka BP.

In between the humid, rainy and warm interglacial intervals, the climate in NE Africa and the Levant became dry and warm, similar to or even drier than the present-day climatic regime. This change is related to the northward shift of the track of the Mediterranean frontal system and the southward shift of the Inter Tropical Convergence Zone and the African/west Asian monsoonal systems. Exceptionally dry spells during interglacial intervals occurred at ~4.2, 5.5, 8.2, ~122, ~215, ~230, ~315, ~330, and ~370 Ka BP.

During glacial intervals the most severe cold and dry conditions prevailed during the LGM at ~19 Ka BP, as well as during intervals that correspond with high-latitude Heinrich events. These include the dry events at ~16, ~24, ~30, ~38, 47–42, ~70, ~145–135, ~275–265, ~300, ~355–340, and ~455–440 Ka BP.

Some cool and humid intervals occur during glacial stages coinciding with enhanced rainfall in the Levant, the formation of a glacial sapropel in the eastern Mediterranean Sea, and the development of a stratified water column in the Red Sea. Milder and more humid conditions in the entire region occur at ~28–25, ~155–152, ~290, and ~345 Ka BP, with overall lower air-temperature compared to the humid interglacial intervals.

In the light of this review, it is important to investigate the relations between milder climate conditions during both glacial and interglacial intervals and the "out-of-Africa" migration of hominids as well as human settlements and their culture in the area.

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References

Adamson, D. A., Gasse, F., Street, F. A. & Williams, M. A. J. (1980). Late Quaternary history of the Nile. *Nature* **288**, 50–55.

Alley, R. B., Mayewski, P. A., Sowers, T., Stuiver, M., Taylor, K. C. & Clark, P. U. (1997). Holocene climatic instability: A prominent, widespread event 8200 yr ago. *Geology* **25**, 483–486.

Almogi-Labin, A. (1982). Stratigraphic and paleoceanographic significance of late Quaternary pteropods from deep-sea cores in the Gulf of Aqaba (Elat) and northernmost Red Sea. *Marine Micropaleontol*ogy **7**, 53–72.

Almogi-Labin, A. (1984). Population dynamics of planktic

Foraminifera and Pteropoda – Gulf of Aqaba, Red Sea. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B Palaeontology* **87**, 481–511.

Almogi-Labin, A., Herut, B., Gavrieli, I., Siman Tov, R. & Schilman, B. (2001). Sapropel events in the eastern Mediterranean Sea as recognized by faunal and geochemical indicators. *Israel Geological Society Annual Meeting, Elat*, Abstract, p. 3.

Almogi-Labin, A., Luz, B. & Duplessy, J.-C. (1986). Quaternary paleo-oceanography, pteropod preservation and stable-isotope record of the Red Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology* **57**, 195–211.

Almogi-Labin, A., Hemleben, Ch., Meischner, D. & Erlenkeuser, H. (1991). Paleoenvironmental events during the last 13,000 years in the Central Red Sea as recorded by pteropoda. *Paleoceanography* **6**, 83–98.

Almogi-Labin, A., Hemleben, Ch. & Meischner, D. (1998). Carbonate preservation and climatic changes in the central Red Sea during the last 380 kyr as recorded by pteropods. *Marine Micropaleontology* **33**, 87–107.

Almogi-Labin, A., Schmiedl, G., Hemleben, Ch., Siman-Tov, R. & Meischner, D. (2000). The influence of the NE winter monsoon on productivity changes in the Gulf of Aden, NW Indian Ocean during the last 530 kyr as recorded by foraminifera. *Marine Micropaleontology* **40**, 295–319.

Arz, H. W., Lamy, F., Pätzold, J., Müller, P. J., & Prins, M. (2003a). Mediterranean moisture source for an early-Holocene humid period in the northern Red Sea. *Science* **300**, 118–121.

Arz, H. W., Pätzold, J., Müller, P. J. & Moammar, M. O. (2003b). Influence of Northern Hemisphere climate and global sea level rise on the restricted Red Sea marine environment during termination I. *Paleoceanography* **18**, 1053.

Auras-Schudnagies, A., Kroon, D., Ganssen, G., Hemleben, Ch. & Van Hinte, J. E. (1989). Distributional pattern of planktonic foraminifers and pteropods in surface waters and top core sediments of the Red Sea, and adjacent areas controlled by the monsoonal regime and other ecological factors. *Deep-Sea Research* **36**, 1515–1533.

Ayalon, A., Bar-Matthews, M. & Kaufman, A. (1999). Petrography, trace elements (Ba, Sr, Mg and U) and isotope geochemistry of strontium and uranium in speleothems as paleoclimate proxies, Soreq Cave, Israel. *Holocene* **9**, 715–722.

Ayalon, A., Bar-Matthews, M. & Kaufman, A. (2002). Climatic conditions during marine isotopic stage 6 in the eastern Mediterranean region as evident from the isotopic composition of speleothems: Soreq Cave, Israel. *Geology* **30**, 303–306.

Bar-Matthews, M. & Ayalon, A. (2003). Climatic conditions in the eastern Mediterranean during the Last Glacial (60–10 ky) and their relations to the Upper Palaeolithic in the Levant as inferred from oxygen and carbon isotope systematics of cave deposits. In (A. N. Goring-Morris & A. Belfer-Cohen, Eds.) *More Than Meets the Eye: Studies on Upper Palaeolithic Diversity in the Near East*. Oxford: Oxbow Books, pp. 13–18.

Bar-Matthews, M., Ayalon, A. Gilmour, M., Matthews, A. & Hawkesworth, C. (2003). Sea-land oxygen isotopic relationships from planktonic foraminifera and speleothems in the eastern Mediterranean region and their implication for paleorainfall during interglacial intervals. *Geochimica et Cosmochimica Acta* **67**, 3181–3199.

Bar-Matthews, M., Ayalon, A. & Kaufman, A. (1997). Late Quaternary paleoclimate in the eastern Mediterranean region from stable isotope analysis of speleothems at Soreq Cave, Israel. *Quaternary Research* **47**, 155–168.

Bar-Matthews, M., Ayalon, A. & Kaufman, A. (1998). Middle to late Holocene (6,500 yr. period) paleoclimate in the eastern Mediterranean region from stable isotopic composition of speleothems from Soreq Cave, Israel. In (A. S. Issar & N. Brown, Eds.) *Water, Environment and Society in Time of Climate Change*. Kluwer Academic Publishers, pp. 203–214.

Bar-Matthews, M., Ayalon, A., Kaufman, A. & Wasserburg, G. J. (1999). The eastern Mediterranean paleoclimate as a reflection of regional events: Soreq Cave, Israel. *Earth and Planetary Science Letters* **166**, 85–95.

Bar-Matthews, M., Ayalon, A. & Kaufman, A. (2000). Timing and hydrological conditions of sapropel events in the eastern Mediterranean, as evident from speleothems, Soreq Cave, Israel. *Chemical Geology* **169**, 145–156.

Bartov, Y., Goldstein, S. L., Stein, M. & Enzel, Y. (2003).

Catastrophic arid episodes in the eastern Mediterranean linked with the North Atlantic Heinrich events. *Geology* **31**, 439–442.

Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J. & Bonani, G. (1993). Correlations between climate records from North Atlantic sediments and Greenland. *Nature* **365**, 143–147.

Calvert, S. E. & Fontugne, M. R. (2001). On the late Pleistocene-Holocene sapropel record of climatic and oceanographic variability in the eastern Mediterranean. *Paleoceanography* **16**, 78–94.

Cember, R. P. (1988). On the sources, formation, and circulation of Red Sea deep water. *Journal of Geophysical Research* **93** (**C7**), 8175–8191.

Cheddadi, R. & Rossignol-Strick, M. (1995). Eastern Mediterranean Quaternary palaeoclimates from pollen and isotope records of marine cores in the Nile cone area. *Paleoceanography* **10**, 291–300.

Clemens, S. C., Murray, D. W. & Prell, W. L. (1996). Nonstationary phase of the Plio-Pleistocene Asian monsoon. *Science* **274**, 943–948.

Clemens, S. C., Prell, W. L., Murray, D. W., Shimmield, G. & Weedon, G. (1991). Forcing mechanisms of the Indian Ocean monsoon. *Nature* **353**, 720–725.

COHMAP Members (1988). Climatic changes of the last 18,000 years: Observations and model simulations. *Science* **241**, 1043–1051.

Degens, E. T. & Ross, D. A. (1969). *Hot Brines and Recent Heavy Metal Deposits in the Red Sea*. New York: Springer-Verlag.

deMenocal, P. B. (1995). Plio-Pleistocene African climate. *Science* **270**, 53–59.

deMenocal, P. B., Ortiz, J., Guilderson, T. & Sarnthein, M. (2000). Coherent high- and low-latitude climate variability during the Holocene warm period. *Science* **288**, 2198–2202.

Edelman-Furstenberg, Y. (1998). Reconstruction of paleoceanographic settings during the late Holocene in the central Red Sea. *Geological Survey of Israel Report* GSI/5/98, 109 pp.

Emeis, K.-C. & Sakamoto, T. (1998). The sapropel theme of Leg 160. In (A. H. F. Robertson, K.-C. Emeis, C. Richter & A. Camerlenghi, Eds.) *Proceedings of the Ocean Drilling Program, Scientific Results* **160**, 29–36.

Emeis, K. C., Sakamoto, T., Wehausen, R. & Brumsack, H.-J. (2000). The sapropel record of the eastern Mediterranean Sea – results of Ocean Drilling Program Leg 160. *Palaeogeography, Palaeoclimatology, Palaeoecology* **158**, 371–395.

Eshel, G. (2002). Mediterranean climates. *Israel Journal of Earth Sciences* **51**, 157–168.

Eshel, G., Cane, M. A. & Blumenthal, M. B. (1994). Modes of subsurface, intermediate, and deep water renewal in the Red Sea. *Journal of Geophysical Research* **99** (**C8**), 15941–15952.

Fairbanks, R. G. (1989). A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature* **342**, 637–642.

Fenton, M., Geiselhart, S., Rohling, E. J. & Hemleben, Ch. (2000). Aplankonic zones in the Red Sea. *Marine Micropaleontology* **40**, 277–294.

Fontugne, M. R. & Calvert, S. E. (1992). Late Pleistocene variability of the carbon isotopic composition of organic matter in the eastern Mediterranean: monitor of changes in carbon sources and atmospheric CO_2 concentrations. *Paleoceanography* **7**, 1–20.

Frumkin, A., Ford, D. C. & Schwarcz, H. P. (1999). Continental oxygen isotopic record of the last 170,000 years in Jerusalem. *Quaternary Research* **51**, 317–327.

Ganopolski, A., Rahmstorf, S., Petoukhov, V. & Claussen, M. (1998). Simulation of modern and glacial climates with a coupled global model of intermediate complexity. *Nature* **391**, 351–356.

Gasse, F. (1977). Evolution of Lake Abhé (Ethiopia and TFAI) from 70,000 B.P. *Nature* **265**, 42–45.

Gasse, F. (2000). Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews* **19**, 189–211.

Gasse, F. & Van Campo, E. (1994). Abrupt post-glacial climate event in West Asia and North Africa monsoon domains. *Earth and Planetary Science Letters* **126**, 435–456.

Geiselhart, S. (1998). Late Quaternary paleoceanographic and paleoclimatologic history of the Red Sea during the last 380,000 years: Evidence from stable isotopes and faunal assemblages. *Tübinger Mikropaläontologische Mitteilungen* **17**.

Goodfriend, G. A. & Magaritz, M. (1988). Paleosols and late Pleistocene rainfall fluctuations in the Negev Desert. *Nature* **332**, 144–146.

Hassan, F. A., 1996. Nile floods and political disorder in early Egypt. In (H. N. Dalfes et al., Eds.) *Third Millennium B.C. Climate Change and Old World Collapse*, NATO ASI Series I, 49. Berlin/Heidelberg: Springer-Verlag, pp. 39–66.

Hassan, F. A. & Stucki, B. R. (1987). Nile floods and climate change. In (M. R. Rampino, J. E. Sanders, W. S. Newman & L. K. Konigsson, Eds.) *Climate: History, Periodicity and Predictability*. New York: Van Nostrand Reinhold, pp. 37–46.

Haynes, C. V. Jr. (1987). Holocene migration rates of the Sudano-Sahelian wetting front, Arba'in Desert, eastern Sahara. In (A. Close, Ed.) *Prehistory of Arid North Africa*. Dallas, TX: Southern Methodist University Press, pp. 69–84.

Haynes, C. V. Jr., Eyles, C. H., Pavlish, L. A., Ritchie, J. C. & Rybak, M. (1989). Holocene palaeoecology of the eastern Sahara: Selima Oasis. *Quaternary Science Review* **8**, 109–136.

Hemleben, Ch., Meischner, D., Zahn, R., Almogi-Labin, A., Erlenkeuser, H. & Hiller, B. (1996). Three hundred eighty thousand year long stable isotope and faunal records from the Red Sea: Influence of global sea level change on hydrography. *Paleoceanography* **11**, 147–156.

Horowitz, A. (1979). *The Quaternary of Israel*. New York: Academic Press.

Imbrie, J., Berger, A. & Shackleton, N. J. (1993). Role of orbital forcing: A two-million-year perspective. In (J. A. Eddy & H. Oeschger, Eds.) *Global Changes in the Perspective of the Past*. New York: John Wiley and Sons, pp. 263–277.

Imbrie, J., Hays, J. D., Martinson, D. G., McIntyre, A., Mix, A. C., Morley, J. J., Pisias, N. G., Prell, W. L. & Shackleton, N. J. (1984). The orbital theory of Pleistocene climate: Support from a revised chronology of the marine $\delta^{18}O$ record. In (A. L. Berger et al., Eds.) *Milankovitch and Climate, Part 1*. Dordrecht: D. Reidel, pp. 269–305.

Jorissen, F. (1999). Benthic foraminiferal successions across Late Quaternary Mediterranean sapropels. *Marine Geology* **153**, 91–101.

Kallel, N., Duplessy, J.-C., Labeyrie, L., Fontugne, M., Paterne, M. & Montacer, M. (2000). Mediterranean pluvial periods and sapropel formation during the last 200,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* **157**, 45–58.

Kallel, N., Paterne, M., Duplessy, J.-C., Vergnaud-Grazzini, C., Pujol, C., Labeyrie, L., Arnold, M., Fontugne, M. & Pierre, C. (1997). Enhanced rainfall in the Mediterranean region during the last sapropel event. *Oceanologica Acta* **20**, 697–712.

Kaufman, A., Wasserburg, G. J., Porcelli, D., Bar-Matthews, M., Ayalon, A. & Halicz, L. (1998). U-Th isotope systematics from the Soreq Cave Israel and climatic correlations. *Earth and Planetary Science Letters* **156**, 141–155.

Klein, B., Roether, W., Manca, B. B., Bregant, D., Beitzel, V., Kovacevic, V. & Luchetta, A. (1999). The large deep water transient in the eastern Mediterranean. *Deep-Sea Research I* **46**, 371–414.

Kroon, D., Alexander, I., Little, M., Lourens, L. J., Matthewson, A., Robertson, A. H. F. & Sakamoto, T. (1998). Oxygen isotope and sapropel stratigraphy in the eastern Mediterranean during the last 3.2 million years. In (A. H. F. Robertson, K.-C. Emeis, C. Richter & A. Camerlenghi, Eds.) *Proceedings of the Ocean Drilling Program, Scientific Results* **160**, 181–190.

Lourens, L. J., Antonarakou, A., Hilgen, F. J., Van Hoof, A. A. M., Vergnaud-Grazzini, C. & Zachariasse, W. J. (1996). Evaluation of the Plio-Pleistocene astronomical timescale. *Paleoceanography* **11**, 391–413.

Matthews, A., Ayalon, A. & Bar-Matthews, M. (2000). D/H ratios of fluid inclusions of Soreq Cave (Israel) speleothems as a guide to the eastern Mediterranean meteoric line relationships in the last 120 ky. *Chemical Geology* **166**, 183–191.

McKenzie, J. A. (1993). Pluvial conditions in the eastern Sahara following the penultimate deglaciation: Implications for changes in atmospheric patterns with global warming. *Palaeogeography, Palaeoclimatology, Palaeoecology* **103**, 95–105.

Meignen, L., Bar-Yosef, O., Mercier, N., Valladas, H., Goldberg, P. & Vandermeersch, B. (2001). Apport des datations au problème de l'origine des Hommes Modernes au Proche-Orient. In (J.-N. Barrandon, P. Guibert & V. Michel, Eds.) *Datation, Actes des XXI rencontres d'archéologie et d'histoire d'Antibes*. APDCA, pp. 295–313.

Milliman, J. D., Ross, D. A. & Ku, T.-L. (1969). Precipitation and lithification of deep-sea carbonates in the Red Sea. *Journal of Sedimentary Petrology* **39**, 724–736.

Olausson, E. (1961). Studies of deep-sea cores. *Reports of the Swedish Deep-Sea Expedition* **8**, 335–391.

Patzert, W. C. (1974). Wind-induced reversal in Red Sea circulation. *Deep-Sea Research* **21**, 109–121.

Reiss, Z., Luz, B., Almogi-Labin, A., Halicz, E., Winter, A., Wolf, M. & Ross, D. A. (1980). Late Quaternary paleoceanography of the Gulf of Aqaba (Elat), Red Sea. *Quaternary Research* **14**, 294–308.

Rindsberger, M., Magaritz, M., Carmi, I. & Gilad, D. (1983). The relation between air mass trajectories and the water isotope composition of rain in the Mediterranean Sea area. *Geophysical Research Letters* **10**, 43–46.

Ritchie, J. C., Eyles, C. H. & Haynes, C. V. (1985). Sediment and pollen evidence for an early to mid-Holocene humid period in the eastern Sahara. *Nature* **314**, 352–355.

Rohling, E. J., Cane, T. R., Cooke, S., Sprovieri, M., Bouloubassi, I., Emeis, K.-C., Schiebel, R., Kroon, D., Jorissen, F. J., Lorre, A. & Kemp, A. E. S. (2002a). African monsoon variability during the previous interglacial maximum. *Earth and Planetary Science Letters* **202**, 61–75.

Rohling, E. J. & De Rijk, S. (1999). Holocene Climate Optimum and Last Glacial Maximum in the Mediterranean: The marine oxygen isotope record. *Marine Geology* **153**, 57–75.

Rohling, E. J., Fenton, M., Jorissen, F. J., Bertrand, P., Ganssen, G. & Caulet, J. P. (1998) Magnitudes of sea-level lowstands of the past 500,000 years. *Nature* **394**, 162–165.

Rohling, E. J. & Gieskes, W. W. C. (1989). Late Quaternary changes in Mediterranean Intermediate Water density and formation rate. *Paleoceanography* **4**, 531–545.

Rohling, E. J., Jorissen, F. J. & De Stigter, H. C. (1997). 200 Year interruption of Holocene sapropel formation in the Adriatic Sea. *Journal of Micropaleontology* **16**, 97–108.

Rohling, E. J., Mayewski, P. A., Hayes, A., Abu-Zied, R. H. & Casford, J. S. L. (2002b). Holocene atmosphere-ocean interactions: Records from Greenland and the Aegean Sea. *Climate Dynamics* **18**, 587–593.

Rossignol-Strick M. (1983) African monsoon, an immediate response to orbital insolation. *Nature* **303**, 46–49.

Rossignol-Strick, M. (1985). Mediterranean Quaternary sapropels, an immediate response of the African monsoon to variation of insolation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **49**, 237–263.

Rossignol-Strick, M. (1999). The Holocene climate optimum and pollen records of sapropel 1 in the eastern Mediterranean, 9000–6000 BP. *Quaternary Science Reviews* **18**, 515–530.

Rossignol-Strick, M., Paterne, M., Bassinot, F. C., Emeis, K.-C. & De Lange, G. J. (1998). An unusual mid-Pleistocene monsoon period over Africa and Asia. *Nature* **392**, 269–272.

Ruddiman, W. F. & Raymo, M. E. (1988). Northern Hemisphere climate régimes during the past 3 Ma: Possible tectonic connections. *Philosophical Transaction of the Royal Society, London* **B318**, 411–430.

Straus, L. G. & Bar-Yosef, O. (Eds.) (2001). Out of Africa in the Pleistocene. *Quaternary International* **75**, 1–130.

Street, F. A. & Grove, A. T. (1976). Environmental and climatic implications of late Quaternary lake-level fluctuations in Africa. *Nature* **261**, 385–390.

Street-Perrott, F. A. & Perrott, R. A. (1993). Holocene vegetation, lake levels, and climate of Africa. In (H. E. Wright, Jr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott & P. J. Bartlein, Eds.) *Global Climate Since the Last Glacial Maximum*. Minneapolis: University of Minnesota Press, pp. 318–355.

Talbot, M. R., Williams, M. A. J. & Adamson, D. A. (2000). Strontium isotope evidence for late Pleistocene reestablishment of an integrated Nile drainage network. *Geology* **28**, 343–346.

Thompson, L. G., Mosley-Thompson, E., Davis, M. E., Henderson, K. A., Brecher, H. H., Zagorodnov, V. S., Mashiotta, T. A., Lin, P-N., Mikhalenko, V. N., Hardy, D. R. & Beer, J. (2002). Kilimanjaro ice core records: Evidence of Holocene climate change in tropical Africa. *Science* **298**, 589–593.

Vaks, A., Bar-Matthews, M., Ayalon, A., Schilman, B., Gilmour, M., Hawkesworth, C. J., Frumkin, A., Kaufman, A. & Matthews, A. (2003). Paleoclimate reconstruction based on the timing of speleothem growth, oxygen and carbon isotope composition from a cave located in the "rain shadow," Israel. *Quaternary Research* **59**, 182–193.

Vergnaud-Grazzini, C., Ryan, W. B. F. & Cita, M. B. (1977). Stable Isotope fractionation, climate change and episodic stagnation in the eastern Mediterranean during the Late Quaternary. *Marine Micropaleontology* **2**, 353–370.

Walter, R. C., Buffler, R. T., Bruggemann, J. H., Guillaume, M. M. M., Berhe, S. M., Negassi, B., Libsekal, Y., Cheng, H., Edwards, R. L., von Cosel, R., Néraudeau, D. & Gagnon, M. (2000). Early human occupation of the Red Sea coast of Eritrea during the last Interglacial. *Nature* **405**, 65–69.

Wehausen, R. & Brumsack, H.-J. (1999). Cyclic variations in the chemical composition of eastern Mediterranean Pliocene sediments: A key for understanding sapropel formation. *Marine Geology* **153**, 161–176.

Weikert, H. (1982). The vertical distribution of zooplankton in relation to habitat zones in the area of the Atlantis II Deep, central Red Sea. *Marine Ecology Progress Series* **8**, 129–143.

Weiss, H., Courty, M. A., Wetterstrom, W., Guichard, F., Senior, L., Meadow, R. & Curnow, A. (1993). The genesis and collapse of third millennium North Mesopotamian civilization. *Science* **261**, 995–1004.

Woelk, S. & Quadfasel, D. (1996). Renewal of deep water in the Red Sea during 1982–1987. *Journal of Geophysical Research* **101**, 18155–18165.

Chapter X

Dental Pathology, Stressful Events, and Disease in Levantine Early Anatomically Modern Humans: Evidence from Qafzeh

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Abstract

Reconstruction of lifestyle and cultural ecology is crucial to the complete interpretation of archaeological populations and must integrate biological studies. Given the scarcity of remains from Paleolithic sites, it is easy to understand that a major question concerns the representativeness of the skeletal samples vis-à-vis the biological population in which they lived. Skeletal samples are indeed biased by different kinds of factors, but they can provide relevant information on the health status of past populations. The unusual concentration of hominid remains in two Middle Paleolithic sites from the Southern Levant, Skhul and Qafzeh, offers the opportunity to evaluate the potential for deriving useful information about Middle Paleolithic societies from bio-archaeological studies. As a majority of the Qafzeh hominids failed to attain reproductive adulthood, we selected the site for conducting a biocultural investigation in order to approach childhood health, nutrition, and aspects of social organization. The purpose of this paper is to contribute to a better understanding of the biology of early modern *Homo sapiens* in the Levant.

Introduction

The Mediterranean Levant has a long and active history of research on Paleolithic archaeology and anthropology. It is a common notion that Upper Pleistocene sites in Southwestern Asia are increasingly critical to our understanding of modern human origins, especially because in the past decade new fossil discoveries and new geological age assessments of the fossil samples have been reported. The Levant, by virtue of its geographic position at the crossroads of Africa and Eurasia, and also because of the human fossils recovered from sites in the region, plays a major role in the debate on the dispersal of modern humans.

Human remains from Skhul and Qafzeh provide physical evidence of early anatomically modern humans (e.g., McCown & Keith 1939; Howell 1958; Vandermeersch 1981; Tillier 1999). These hominids were the bearers of Mousterian lithic industries that are dated to more than 90 Ka BP (Schwarcz et al. 1988; Valladas et al. 1988; Grun & Stringer 1991). The association of early modern humans with Middle Paleolithic technologies suggests that morphological "modernization" preceded behavioral "modernization" in the Levant. Indeed, the pattern of population change in the region did not parallel that of Europe, where the first modern humans were associated with Upper Paleolithic assemblages.

The relationships of the first Levantine modern humans to their successors in the region are still unclear, because it can be established from archaeological, paleontological, and geological data that 60 Ka separate the Skhul and Qafzeh hominids from the Upper Paleolithic modern humans found in Qafzeh and Ksar 'Akil (Belfer-Cohen & Bar Yosef 1981; Mellars & Tixier 1989; Bergman & Stringer 1989; Tillier & Tixier 1991; Vandermeersch & Arensburg, manuscript in preparation).

The study of the evolutionary events related to modern human origins and their subsequent dispersal is based upon different sources of data. The integration of biological with cultural data can help us understand prehistoric human behavioral capabilities. Identification of skeletal abnormalities and degenerative joint disease, as well as evidence for bone lesions caused by trauma, can provide insights into adaptive patterns in prehistoric populations. Dental and skeletal indicators of stressful events provide an intimate look at adaptations of individuals and populations attributable to biological, environmental, and cultural factors, although it is well known from the study of living populations that stress is experienced differentially by individuals due to differences in their reaction to exposure to environmental rigors, infections, and nutritional deficiency.

Useful information about Middle Paleolithic societies can be obtained from bio-archaeological studies. Investigating human paleobiology is a way to understand childhood health, nutrition, and level of social organization. The purpose of this paper is to contribute to a better knowledge of the biology of early modern *Homo sapiens* in the Levant.

Material

Two Middle Paleolithic sites of the Southern Levant, Skhul and Qafzeh, show a spatial and temporal concentration of hominid remains that is intriguing. The hominid sample preserves infants and children, as well as young and old adults, that are commonly accepted as early representatives of anatomically modern humans dated to more than 90 Ka BP. Methodological difficulties inherent in accurately estimating the age distribution of the adults, as well as the sample size (MNI=25), limit the possibility of constructing a mortality profile and examining the morbidity of the original population. However, this skeletal material raises the question of the health status of the human group preserved and is crucial for understanding biological, chronological, and cultural aspects of ancient *Homo sapiens* in the context of the Levantine Middle Paleolithic. Furthermore, most of the intentional burials in the region were found in Skhul and Qafzeh, and some of them document complex mortuary practices applied to unhealthy individuals (e.g., McCown & Keith 1939; Vandermeersch 1970; Tillier et al. 1988; Hovers et al. 1995).

One major difference between the Skhul and Qafzeh samples lies in the age-at-death distribution of the individuals. Indeed, a majority of the Qafzeh hominids fail to attain reproductive adulthood (Vandermeersch 1981; Tillier 1999), while remains of only three juveniles were recovered from Skhul (McCown & Keith 1939). In demographic studies, the frequency of children is an important component in evaluating the social and sanitary conditions of a community (e.g., Saunders 1992; Saunders & Herring 1995; Sellier 1995). The Qafzeh juvenile sample consists of eight individuals with two infants (less than one year old at death) and six children from ca. 3 years to adolescence (Tillier 1999). Following Vandermeersch (1981, manuscript in preparation), it is not possible to determine how old each of the adults was at death. Nevertheless, it may be assumed that one young adult (Qafzeh 5) and five older adults (Qafzeh 3, 6, 7, 8, and 25) were present, while Qafzeh 9 was between adolescence and adulthood (age class 15–19 years).

Aspects of the archaeological record

At Qafzeh, the spatial distribution of the hominid remains is restricted to a few square meters in front of the entrance to the cave and is associated with layers XV, XVII, and XXIII. While a majority of the human remains originated from layer XVII, the stratigraphic sequence covers a short time span, as shown by the TL dates (Valladas et al. 1988). In connection with this temporal and spatial distribution, a working hypothesis concerns the representativeness of the human sample and the possible relationships between individuals of the group.

The human remains originated from the lower layers of the entrance zone of the site that contain a low density of lithic artifacts, a huge assemblage of micromammals, and a few hearths. The lithic assemblage is described as a "Tabun C-type" Mousterian industry (Boutié 1989; Hovers 1997), in which centripetal and/or bi-directional preparations prevail and the typical products are side scrapers, large oval and quadrangular Levallois flakes.

The animal community is rich in microvertebrates and, as reported by Tchernov (1995:178), the assemblage is "clear evidence for a northward expansion of the African and Saharo-Arabian biotic zone." With regard to the nature of human occupation, the predominance of micromammals, on the one hand, suggests a period "when the site was used only occasionally for special activities" (Bar-Yosef 2000:122); whereas, on the other hand, the presence of commensal mice and African rats might point to long-term human occupation (Tchernov 1984, 1998).

Evaluating the organization of space and activities in Qafzeh appears rather difficult given that the archaeological record, most especially the fauna, has been severely impacted by brecciation of the layers. We have to consider, indeed, that the faunal assemblage that has been preserved does not faithfully reflect either the surrounding habitat or the human diet. Bar-Yosef (1989, 1993) suggested that a basecamp might have been located somewhere near the cave, and that the inhabitants used Qafzeh Cave as their burial ground.

The Mousterian sequence in the entrance zone is, indeed, rich in human remains, but the fossil sample is relatively small. There is no theoretical basis for estimating either the maximum life expectancy of the Qafzeh early modern humans or the size of the human group that used the site. However, study of the skeletal anomalies and pathologies in the Qafzeh hominid sample can reveal aspects of the social life of the people that cannot be directly inferred from the archaeological record.

Dental health and oral hygiene in the Qafzeh hominids

Most of the dental disease patterns in human populations are related to the interaction between diet and microorganisms that live in the mouth. There are many topics of potential investigation in dental anthropology that are related to the morphology of teeth, pathologies, and behavioral aspects occurring per vitam (during the life of individuals). Such morphological changes, indeed, have to be clearly separated from those resulting from postmortem chemical or physical alterations related to fossilization or human manipulation during excavations. Observation of the physical condition of the dentition can provide valuable information concerning an individual's health status and can illuminate living conditions, such as nutrition and cultural habits.

At Qafzeh, within the non-adult cohort, a total of 68 deciduous teeth and 107 permanent teeth are preserved, and Qafzeh 4, 9, 10, 11, and 15 preserved virtually complete dentitions. While the Qafzeh adults provide data on 102 teeth, only two of the individuals (Qafzeh 7 and 25) retain most of their teeth and Qafzeh 6 preserves its upper dental arcade. Such information related to oral biology is seldom observed in Levantine Middle Paleolithic sites due to the high percentage of missing teeth, both antemortem and postmortem. In addition to studies of the distribution of anomalies and pathologies on complete dental arches, useful information can also be obtained by examining fragmentary dentitions and isolated teeth.

Based on the examination of complete dental arches without secondary alteration resulting from postmortem processes, there is no evidence at Qafzeh of malocclusion, crowding, or abnormal spacing of teeth. Rotation of single teeth was observed in a few cases: mesio-buccal rotation of the right second molar in the Qafzeh 15 mandible, mesio-lingual rotation of the left lower second premolar in Qafzeh 11 (Tillier 1999).

Taking into consideration the classification of dental diseases proposed by Lukacs (1989), we consider three categories of tooth modification – developmental, infectious, and degenerative. In addition, evidence for alveolar bone remodeling and periodontal disease are examined.

Periodontal diseases and antemortem tooth loss

There is little evidence of dental health problems in the Qafzeh hominids, and most of the adult individuals manifest normal occlusal attrition of the teeth. By contrast, Qafzeh 3 provides evidence of considerable attrition in two upper anterior teeth, the right incisors (Figure 1C2), with the dentine largely exposed on the occlusal surface and the crown height reduced. Three posterior teeth from the same adult specimen (left premolars and third molar) are less worn.

Bacterial tooth deposits (dental plaque) are the principal cause of periodontal disease and a major factor in the loss of teeth in early and late adulthood in past populations. However, in Qafzeh both antemortem tooth loss and periodontal disease are rather exceptional, as far as we can tell from the human remains that are preserved.

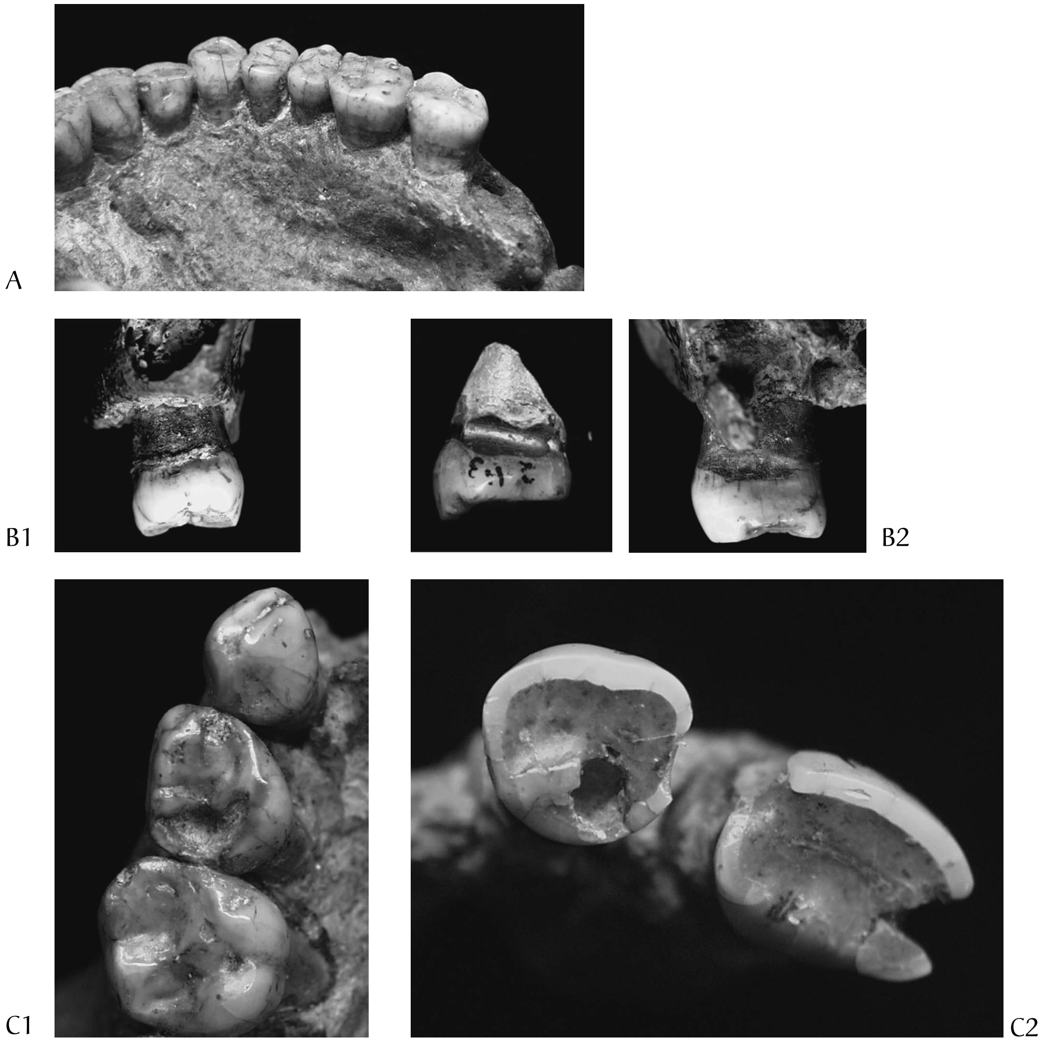

Figure 1. Aspects of oral health in the Qafzeh hominids. A. Periodontitis in the adult Qafzeh 6 maxilla; B. Calculus (1) and interproximal wear groves (2) in the upper teeth of Qafzeh 3; C. Occlusal caries in the upper deciduous molar of Qafzeh 4 (1) and upper incisor of Qafzeh 3 (2).

Within the adult sample, the maxillary bone of one specimen, Qafzeh 6, manifests antemortem tooth loss (the left third molar) and, in addition, a process reactive to bone resorption (Figure 1A) that can be qualified as "peripheral buttressing effect" on both buccal and lingual sides (periodontitis). Periodontal recession can also be observed on both maxillary and mandibular alveolar regions in the adult Qafzeh 8, at the level of the alveolar crests. No evidence of dental calculus deposition can be seen on the teeth of the Qafzeh 6 and 8 individuals, but this might be the result of intensive cleaning after the discovery of the specimens. By contrast, an isolated upper third molar from Qafzeh 3 exhibits dental calculus accumulation (Figure 1B1) on the distal surface of the crown, near the cervix.

Evidence of tooth care or occupational modification?

Studies in dental anthropology have shown that various forms of manipulation in the oral region can cause accidental dental modifications. Within the Qafzeh hominid group, Qafzeh 3 provides evidence of interproximal grooves in the distal surface of the two first upper premolars and in the mesial surface of the third right molar (Figure 1B2). Such smoothly polished wear grooves in upper teeth might suggest either repeated use of a tooth pick to remove food particles (tooth care) or, especially in the case of the two first premolars, other types of manipulation associated with specific occupational activities of the individual. SEM images of the wear-facets in the interproximal tooth surfaces should help to elucidate the nature of personal habits involved in such specific artificial modifications of the Qafzeh 3 teeth.

Search for carious lesions

According to current scientific knowledge, the development of carious lesions depends on genetic and environmental factors, as well as socio-cultural influences. The fact that Middle Paleolithic populations exhibit few caries (e.g., Boydstun et al. 1988; Tillier et al. 1995; Trinkaus et al. 2000) has led some scholars to believe there was an immunity to carious development in primitive societies. Others are of the opinion that the increase of caries after the Paleolithic period may be the consequence of both the spread of agriculture, when food became rich in carbohydrates, and the increase in human life span (e.g., Larsen 1983; Smith et al. 1984).

Only occlusal caries can be identified in three of the Qafzeh individuals, some affecting the deciduous dentition, others being on permanent teeth. Small occlusal caries are present on the first upper deciduous molars of the Qafzeh 4 child, ca. 7 years old at death (Figure 1C1). Among the adults, two cases can be reported: a central permanent upper incisor from the adult Qafzeh 3 (Boydstun et al. 1988, Figure 1C2), and probably a permanent upper right molar from the Qafzeh 7 adult specimen.

Indicators of non-specific stress and growth disturbances

Unique insights into the health status of past populations come from a consideration of the analysis of growth disturbances and developmental stress. Patterns of bone growth and remodeling can be used to interpret the nature of physiological disruptions at different times during the life of an individual. During the growth phase of long bones, active remodeling dynamics at the proximal and distal ends of the diaphysis can be altered by several factors. Such bone alteration can be identified with the manifestation of growth arrest lines (Harris Lines) above the metaphyseal region of the bones. There are other indicators of non-specific stress (e.g., cribra orbitalia, porotic hyperostosis) affecting the orbital roof and cranial bones that are clearly distinguishable from pseudopathologies resulting from postmortem sources and they are commonly associated with anemia and rickets. However, the etiology of such inflammatory changes of the original compact bone is still debated (Wapler & Schultz 1996).

Developmental tooth enamel defects

Severe patterns of pathological alterations of the dental enamel, such as transverse linear enamel hypoplasia, are currently employed to assess physiological stress and growth disturbances during childhood (Goodman & Rose

1990). Prevalence of developmental enamel defects in deciduous dentition is correlated with developmental disorders in intra-uterine and postnatal growth and nutritional status of infants. In the literature, methods for the evaluation, classification, and etiology of enamel defects have been discussed (e.g., Neiburger 1990; Goodman 1991). Only a few reports have been devoted to Middle Paleolithic hominids (Molnar & Molnar 1985; Ogilvie et al. 1989; Brennan 1991; Skinner 1996).

Among the Qafzeh hominids, dental alterations associated with non-specific physiological stress are scarce. In the two Qafzeh infants (13 and 14) there are no signs of developmental disorders in the enamel. Skinner (1996, Tables 1 and 6) for the Qafzeh 11 adolescent reported three affected teeth and mentioned hypoplastic defects located at mid-crown height of the lower right and left M_1, just apical to the cusp tip in the second lower right M_2; we fail to confirm these observations. We observed no manifestations of transverse linear enamel hypoplasia on the deciduous and permanent dentitions of the Qafzeh children. Such pathological alteration of the tooth crown was recognized on a single adult permanent tooth (an isolated lower canine, A14-CXVI) that exhibits three lines located between 3.2 and 5.0 mm above the cervix. Estimating the age at which the dental enamel defects occurred remains uncertain given the lack of a reliable method designed specifically for Paleolithic populations and on the basis of one tooth. While serious hypoplastic enamel defects are exceptional in the hominid sample, it would be quite inappropriate to conclude that the Qafzeh individuals never suffered from an acute phase of disease during infancy or childhood.

Infant mortality

At Qafzeh, remains of two individuals under one year of age (Qafzeh 13 and 14) were recovered, but it is evident that neonatal mortality rates (deaths at birth or in the first four weeks) and post-neonatal mortality (deaths between four weeks and the end of the first year) were certainly higher among Middle Paleolithic human communities than among later ones. From the most complete specimen, Qafzeh 13, cranial and postcranial fragmentary bones and a few germs of deciduous teeth are preserved. Incidence of periosteal reactive bone (porotic hyperostosis) can be identified on this neonate, involving the outer table of cranial bones (e.g., parietal and sphenoid regions) as well as fragments of the ulna, ilium, and vertebrae. No indication of defects in dental development can be recognized on the tooth germs and a similar conclusion is reached through examination of seven isolated primary teeth preserved from Qafzeh 14 (ca. 6 months at death).

On the basis of these observations, it might be suggested that most of the deceased juveniles (with the exception of Qafzeh 13) represent sub-adult individuals that survived to early childhood and/or died before the skeleton had had time to respond to chronic diseases. Variation in dental age relative to skeletal size remains difficult to assess from the fossil record and the preservation of the long bones. Developmental defects in postcranial bones can be seen in two cases associated with pathologies that will be presented later.

Soft tissue lesions and tumors of osseous origin

The study of skeletal abnormalities is important in the understanding of the health of ancient populations and their genetic and immunological status. It can also be indicative of individual adaptation to environmental conditions as well as to certain cultural behaviors.

Lesions of the ear

The adolescent Qafzeh 11, ca. 13 years old at death according to modern human reference standards (based on tooth development and bone ossification), manifests some striking cranial abnormalities indicating that the individual experienced various degrees of bone lesions.

On the left side of the skull, the temporal bone exhibits an opening of the mastoid cells as shown by x-rays (Figure 2B), indicating a development of the infection within the mastoid process. In addition, two of the ear ossicles (the malleus and incus) are preserved, and they manifest

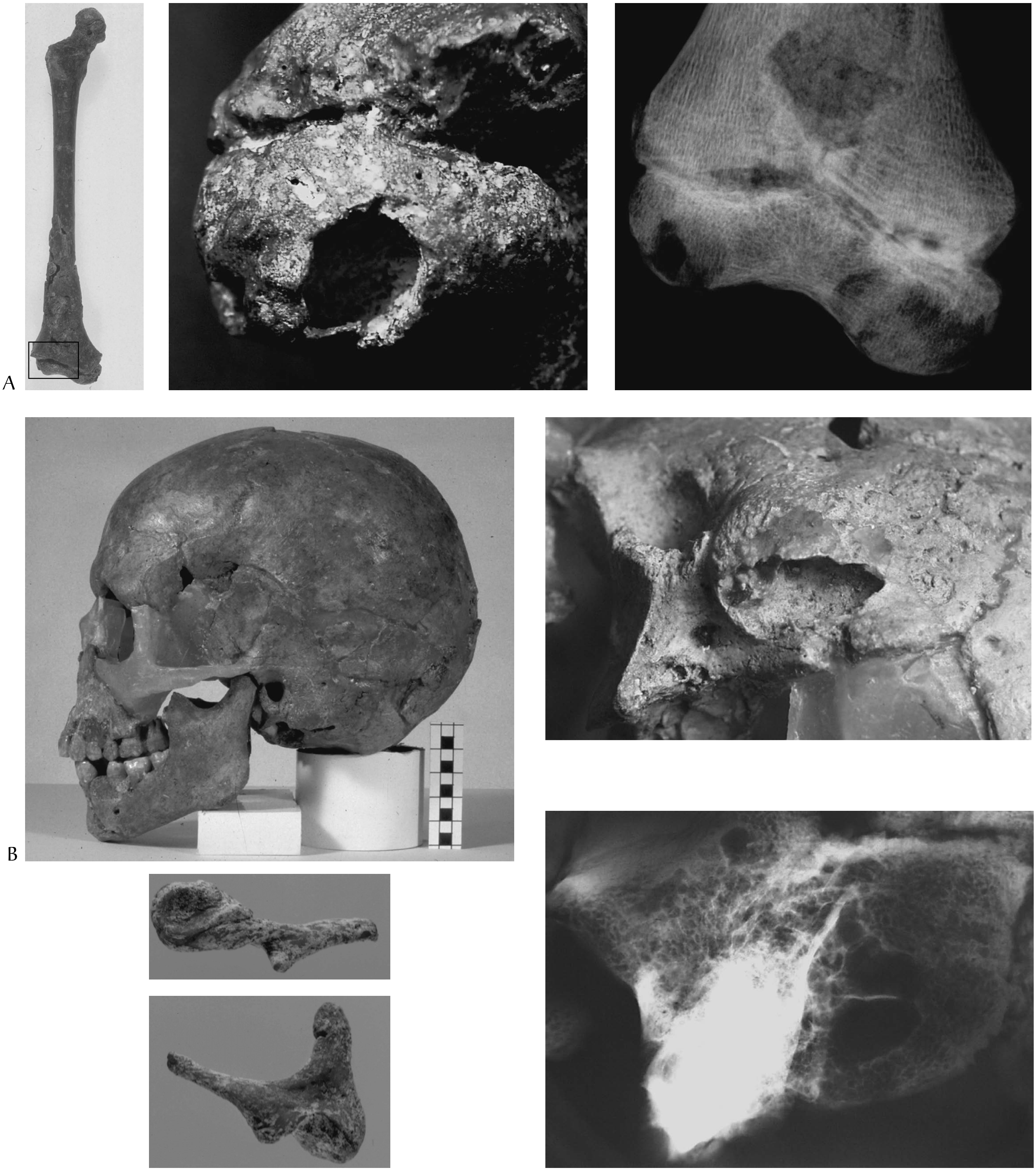

Figure 2. Soft-tissue lesions and tumor of osseous origin. A. Ostoid osteoma in the lateral epicondyle of the right femur in the Qafzeh 10 child (ca. 6 years old); B. *Otitis media* in the left temporal bone of the adolescent Qafzeh 11 that has affected the two middle ear ossicles.

antemortem erosion (Nathan & Arensburg 1972). The bone alteration is located on the distal parts of the malleus handle and the incudal long process. Such data suggest the occurrence of an inflammatory disorder in the ear during life and the diagnosis of chronic *otitis media* in the Qafzeh 11 adolescent.

An extensive infection of the middle ear is primarily a disease of children and such an inflammatory ear disorder is compatible with life, but the archaeological record of ear infection is extremely poor among prehistoric populations. The occurrence of chronic *otitis media* in the Qafzeh 11 adolescent presented here is unique within the Middle Paleolithic juvenile hominid sample.

Long bone lesions

Identification of bone lesions that arise in young growing individuals in prehistoric populations is rather difficult, as it is uncommon to recover the joint surfaces that would allow a more complete diagnosis of pathological conditions or infection than is possible with dense bone shafts. Such a state of preservation is found within the Qafzeh immature cohort in a unique case, Qafzeh 10, a child ca. 6 years old at death.

The right femur of this individual is complete (but partially crushed postmortem) and provides evidence of irregular skeletal morphology in its distal epiphysis. This bone manifests a small rounded tumor (10.3 x 7.8 mm) on the lateral epicondyle which appears as a radiolucent area on the x-rays (Figure 2A). These features are characteristic of an osteoid osteoma, a benign skeletal tumor.

Radiological examination of the distal femur and proximal tibia provides indications of growth arrest lines (Harris lines) that are incompletely preserved on the femoral diaphysis due to postmortem morphological change. Such lines located just above the metaphyseal region indicate that the child had recovered from a stressful event that could be directly correlated to the skeletal tumor mentioned above or to another physiological insult received by the same individual that will be presented later.

Cranial malformations

Craniosynostosis

Closure of the cranial vault sutures normally takes place during adult life. As reported by Aufderheide & Rodriguez-Martin (1998:52), premature fusion of the cranial sutures "can occur as isolated conditions or forming part of polytropic syndromes" and can change the normal shape of the skull.

The Qafzeh 10 child manifests premature closure of the suture between the frontal and parietal bones on the right side of the skull, 2 cm from bregma (Figure 3A). This asymmetrical craniosynostosis, which occurred at an abnormally early age, was associated with the presence of two other unusual traits: a trapezoid-shaped elevation of the bregmatic region and a surrounding depression affecting the outer table of the parietal and frontal bones. As a result, the skull appears elongated and vertically flat with a lateral and antero-posterior asymmetry. The nature of the underlying mechanisms that produced the skull anomalies in Qafzeh 10 is unknown, but this might be a secondary reaction to other processes correlated to minor injury. It is important to point out that only some of the craniosynostosis cases in recent populations can be assigned to a specific etiology (Maroteaux 1982; Aufderheide & Rodriguez-Martin 1998). In the case of the Qafzeh 10 child, suture closure was limited to 3.7 cm and apparently had no influence on the development of the cranial capacity.

Hydrocephalus

Gross analysis of the Qafzeh 12 skeleton and examination of a few x-ray images indicate that this ca. 3-year-old child did not undergo normal development (Tillier 1999; Tillier et al. 2001). As previously reported, the skull manifests several notable skeletal abnormalities that indicate hydrocephalus: (1) strong indication of an enlargement of the skull, especially in the frontal and parietal regions, (2) very large and asymmetric anterior fontanelle at the junction of the metopic, coronal, and sagittal sutures, and (3) pronounced asymmetry in the occipital bone that seems to be the result of differential development of the cerebral hemispheres.

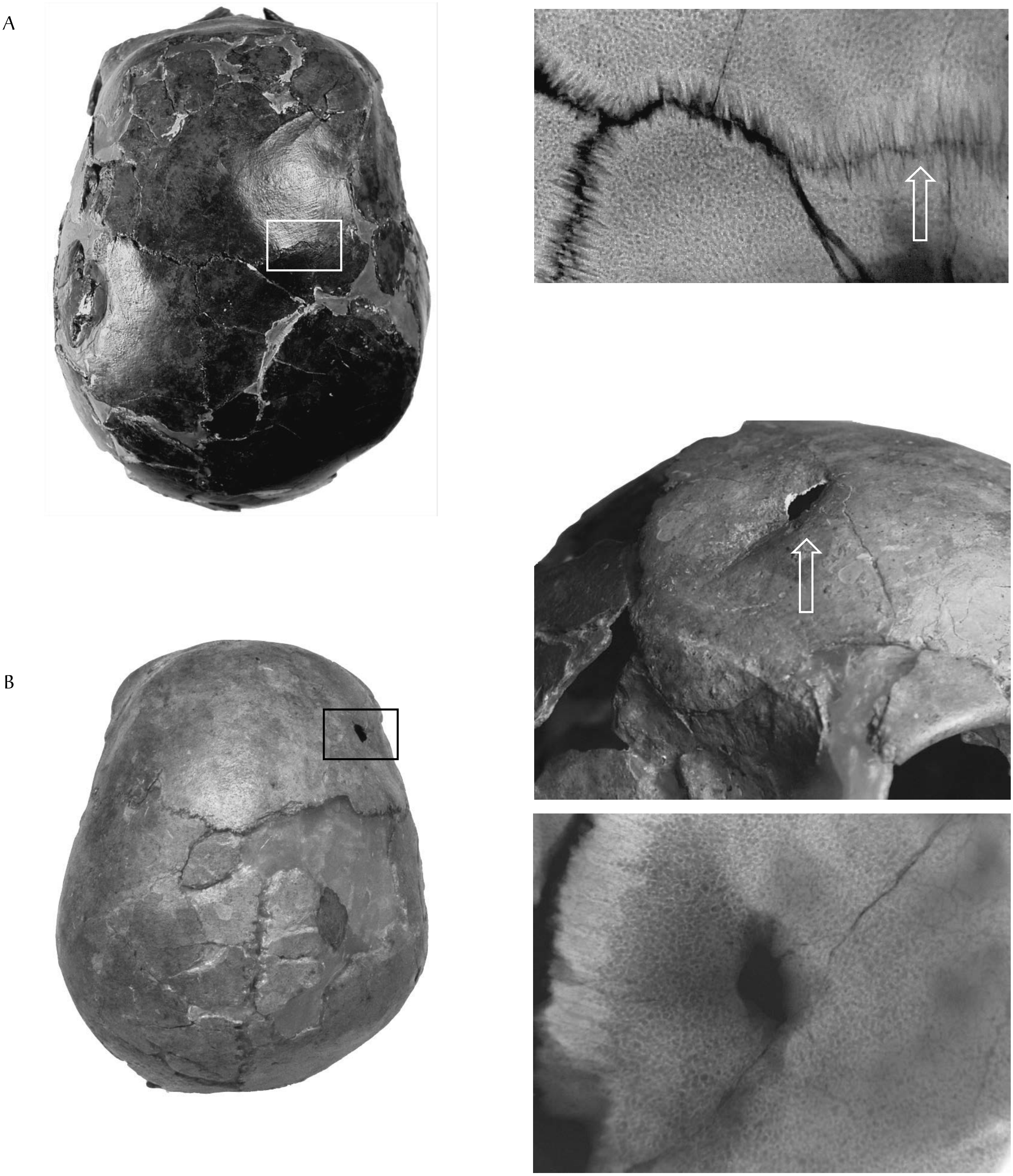

Figure 3. Cranial malformation and trauma. A. Right premature closure of the coronal suture in the Qafzeh 6 child (ca. 6 years old); B. Traumatic lesion in the right side of the frontal bone in the Qafzeh 11 adolescent.

The child's skeleton is only partially preserved, but a few skeletal elements suggest developmental defects in the postcranial bones (vertebrae, long bones). There is some indication of reduction in the size of the transverse diameter of the cervical and thoracic vertebral canals. The extreme gracility and shortness of the shafts in the upper limb, with thin cortical bone and medullar canal radiolucence in a radiographical examination, contrast with those of normal children (Maresh 1943, 1955).

Hydrocephalus results from the increased production or decreased absorption of cerebrospinal fluid, or from blockage of one of the normal outflow pathways of the ventricular system. The most common forms occur in young children but archaeological cases of hydrocephalus have seldom been observed (Brothwell & Sandinson 1967; Ferembach 1968; Ortner & Putschar 1985; Richard & Anton 1991), and all of them belong to relatively recent historic times. The Qafzeh 12 individual documents an early case of hydrocephalus among Paleolithic populations, and without proper surgical treatment, the child died in early childhood.

Skeletal evidence of trauma

The number of Qafzeh individuals documenting the presence of antemortem trauma is rather limited. The Qafzeh 6 adult skull shows in its left supra-orbital region a concave indentation of the outer table of the frontal bone, without a fracture. Such a condition may result from sudden head movements, a blow to the head, or an episode of some sort of interpersonal violence.

According to Dastugue (1981), one adult individual, Qafzeh 8, exhibits traces of past injury in his left foot represented by a fracture of the calcaneus and consecutive arthrosis in the articular surfaces between the talus and calcaneus. Such a diagnosis led the author to conclude that Qafzeh 8 probably had reduced and painful locomotion. However, from preliminary observations made on the original bones, it appears that the diagnosis of a traumatic event needs to be revised (Tillier et al., manuscript in preparation)

Within the non-adult sample, the Qafzeh 11 adolescent provides evidence of a serious lesion resulting in a pathological change in the cranial vault (Figure 3B). The pathology is characterized by a depressed bone lesion on the right side of the frontal squama, with postmortem disappearance of a small portion of the thin bone. With regard to the overall form of the bone lesion and x-ray examination, the diagnosis of traumatic skeletal injury seems to prevail over that of an epidermoid bone cyst. The nature of the impacting object is unknown. The healing response had not undergone its complete trajectory before the death of the adolescent.

Conclusions

Investigating dental defects of immature Paleolithic hominids, Skinner (1996:833) reported that "the major contrast between the Middle and Upper Paleolithic in terms of enamel hypoplasia is the advent of stressful episodes in early infancy in the Upper Paleolithic." The Upper Paleolithic hominid sample investigated by Skinner consisted of early modern humans from Western Europe. The evidence for "significantly more stress" at a younger age within this Upper Paleolithic sample could be related to "population expansion which could at some point have led to nutritional and demographic stress" (Skinner 1996:848).

From our analysis of the dentition, it appears that physiological stress is not recorded in the non-adult cohort from Qafzeh and can be observed on a single adult tooth. Comparative data from the Skhul hominids are not available at the present time, except for a preliminary report made by Sognnaes (1956:549–550) on two permanent molars belonging to the Skhul II adult specimen. From these observations, and the low frequency of dental caries recorded within both the Skhul and Qafzeh samples, we do not argue that the teeth of these hominids had a superior enamel developmental structure to those of later populations. By no means can we conclude on the basis of the available evidence that these prehistoric foragers experienced no stress in infancy and later development.

Although the Levant provides the best case for the Mousterian/Early Modern Human association, behavioral models are still employed in the current debate concerning the origin and dispersal of modern humans. Studies of skeletal biology add to archaeological reconstructions by providing insights into the lifeways of ancient populations through the analysis of health and nutrition.

The Qafzeh human remains provide little evidence of trauma and injuries and, in this aspect, our data are in agreement with the previous conclusions reached by McCown and Keith in 1939 on the health status of the Skhul people. However, differences between adult and non-adult cohort morbidity care are observed within the Qafzeh hominid sample. The mortality profile in which more than fifty percent are sub-adults is unusual for any Paleolithic sample with many skeletal remains. This is not meant to imply that the percentage of children reveals a change in population parameters or the overall pattern of mortality. The fact that four of the Qafzeh children show infection and significant pathologies may document a social peculiarity 100,000 years ago in the Levant (i.e., that the Qafzeh people had compassion for unhealthy children), and the presence of burials strengthens the suggestion of Bar-Yosef (2000) with regard to the use of the site for special activities.

At Qafzeh, the importance of children can be deduced from the special care given to unhealthy individuals that was maintained until their death, and the occurrence of intentional burials in the site. Furthermore, the non-adult sample provides evidence of specific funerary practices applied to some of the individuals, including change in burial pattern and grave goods (Vandermeersch 1969, 1970; Tillier 1995).

Several lines of evidence suggest that severe chemical disturbances have affected the Qafzeh Mousterian layers (Bar-Yosef & Vandermeersch 1981; Vandermeersch 1981). Consequently, recovery of either large parts of a human skeleton or skeletons in anatomical connection cannot be interpreted as simply depositional accidents (*contra* Gargett 1999). However, we must admit that, in the case of Qafzeh 13 (neonate) and Qafzeh 12 (hydrocephalus, ca. 3-year-old child), there are no field observations that could be employed to reconstruct elements in the sequence of placement of the bodies.

In contrast, the taphonomic approach provides us with more complete information about the mortuary practices applied to the Qafzeh 10 and 11 children. The Qafzeh 10 child (ca. 6 years old at death with a craniosynostosis) was buried together with an older individual, Qafzeh 9 (age class 15–19 years), and this simultaneous inhumation is unique among Levantine Middle Paleolithic sites. The body of the child was deposited near the feet of the older individual: simultaneous deposition of the two individuals is supported by the close spatial relationships between the two skeletons and the lack of disturbance of Qafzeh 9 labile foot articulations (i.e., looser ligamentous connections disarticulating earlier in body decomposition). The association of Qafzeh 9 with the child is very intriguing, and we hope that a re-examination of the skeleton will contribute to a better understanding of this simultaneous deposition (Tillier et al. in prep.).

The Qafzeh 11 burial provides an interesting example of death ritual: the body of this adolescent was accompanied by an offering represented by parts of deer antlers that were arranged near the face and hands (Vandermeersch 1970). Such a ritual practice, applied to a young individual who suffered from a cranial trauma, is a reflection of elaborated social behavior among the Qafzeh people. Following on this, it is interesting that, besides mortuary practices, other important evidence of symbolic activities comes from engraved pieces of red ochre (Vandermeersch 1966) and a broken Levallois core (Hovers et al. 1997), as well as perforated marine shells (Bar-Yosef 1989; Taborin 2003).

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References

Arensburg, B., Nathan, H. (1972). A propos de deux osselets de l'oreille moyenne d'un Néandertaloïde trouvés à Qafzeh (Israël). *L'Anthropologie*, **76**, 301–307.

Aufderheide, A. C. & Rodriguez-Martin, C. (1998). *The Cambridge Encyclopedia of Human Paleopathology.* Cambridge: Cambridge University Press.

Bar-Yosef, O. (1989). Upper Pleistocene cultural stratigraphy in Southwest Asia. In (E. Trinkaus, Ed.) *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*. Cambridge: Cambridge University Press, pp. 154–180.

Bar-Yosef, O. (1993). Site formation processes from a Levantine viewpoint. In (P. Goldberg, D. T. Nash & M. D. Petraglia, Eds.) *Formation Processes in Archaeological Sites*. Madison, WI: Prehistory Press, pp. 13–32.

Bar-Yosef, O. & Vandermeersch, B. (1981). Notes concerning the possible age of the Mousterian layers in Qafzeh Cave. In (J. Cauvin & P. Sanlaville, Eds.) *Préhistoire du Levant*. Colloques Internationaux du CNRS 59. Paris: Editions du CNRS, pp. 281–285.

Belfer-Cohen, A. & Bar-Yosef O. (1981). The Aurignacian at Hayonim Cave. *Paléorient* **7**, 19–42.

Bergman, C. & Stringer, C. B. (1989). Fifty years after: Egbert, an early Upper Palaeolithic juvenile from Ksar Aqil, Lebanon. *Paléorient* **15**, 99–111.

Boutié, P. (1989). Etude technologique de l'industrie Moustérienne de la grotte de Qafzeh (près de Nazareth, Israël). In (O. Bar-Yosef & B. Vandermeersch, Eds.) *Investigations in South Levantine Prehistory*. BAR International Series 497. Oxford: British Archaeological Reports, 213–229.

Boydstun, S. B., Trinkaus, E. & Vandermeersch, B. (1988). Dental caries in the Qafzeh 3 early modern human. *American Journal of Physical Anthropology* **75**, 188–189.

Brennan, M. U. (1991). *Health and Disease in the Middle and Upper Paleolithic of Southwestern France*. Unpublished PhD Dissertation, New York University.

Brothwell, D. R., Carbonell, V. M. & Goose, D. H. (1963). Congenital absence of teeth in human populations. In (D. R. Brothwell, Ed.) *Dental Anthropology*. New York: MacMillan, pp. 179–190.

Brothwell, D. R. & Sandinson, A. T. (Eds.). (1967). *Diseases in Antiquity: A Survey of the Diseases, Injuries and Surgery of Early Population.* Springfield: Charles C. Thomas.

Dastugue, J. (1981). Pièces pathologiques de la "nécropole" Moustérienne de Qafzeh. *Paléorient* **7**, 135–140.

Duday, H. & Arensburg, B. (1991). La pathologie. In (O. Bar-Yosef & B. Vandermeersch, Eds.) *Le Squelette Moustérien de Kebara*. Cahiers de Paléoanthropologie. Paris: Editions du CNRS, pp. 179–193.

Ferembach, D. (1968). Un crâne Néolithique hydrocéphale du Portugal. In *Anthropologie und Humangenetik: Festschrift Zum 65 Geburtstag von Professor Dr. Karl Saller*. Stuttgart: Gustave Fischer Verlag, pp. 136–141.

Gargett, R. (1999). Middle Palaeolithic burial is not a dead issue: The view from Qafzeh, Saint-Césaire, Kebara, Amud and Dederyeh. *Journal of Human Evolution* **37**, 27–90.

Goodman, A. H. & Rose, J. C. (1990). Dental enamel hypoplasias as indicators of nutritional status. *Yearbook of Physical Anthropology*. New York: Wiley Liss, pp. 279–293.

Grolleau Raoux, J.-L., Crubézy, É., Rouge, D., Brugne, J.-F. & Saunders, S. H. (1997). Harris lines: a study of age-associated bias in counting and interpretation. *American*

Journal of Physical Anthropology **103**, 209–217.

Grün, R. & Stringer, C. B. (1991). Electron spin resonance dating and the evolution of modern humans. *Archaeometry* **33**, 153–199.

Hovers, E. (1997). *Variability of Levantine Mousterian Assemblages and Settlement Patterns: Implications for the Development of Human Behavior*. Unpublished PhD Dissertation, Hebrew University of Jerusalem.

Hovers, E., Rak, Y., Lavi, R. & Kimbel, B. (1995). Hominid remains from Amud Cave in the context of the Levantine Middle Paleolithic. *Paléorient* **21**, 47–62.

Hovers, E., Vandermeersch, B. & Bar-Yosef, O. (1997). A Middle Paleolithic engraved artefact from Qafzeh Cave, Israel. *Rock Art Research* **14**, 79–87.

Howell, F. C. (1958). Upper Pleistocene men of the Southwestern Asian Mousterian. In *Hundert Jahre Neanderthaler Neandertal Centenary 1856–1956*. Köln-Graz: Böhlau Verlag, pp. 185–198.

Larsen, C. S. (1983). Biobehavioral implications of temporal change in cariogenesis. *Journal of Archaeological Science* **10**, 1–8.

Maresh, M. M. (1943). Growth of major long bones in healthy children: A preliminary report on successive roentgenograms of the extremities from early infancy to twelve years of age. *American Journal of Diseases of Children* **66**, 227–257.

Maresh, M. M. (1955). Linear growth of long bones of extremities from infancy through adolescence. *American Journal of Diseases of Children* **89**, 725–742.

Maroteaux, P. (1982). *Maladies Osseuses de l'Enfant*. Paris: Flammarion, Coll. Médecine Sciences.

Mellars, P. & Tixier, J. (1989). Radiocarbon accelerator dating of Ksar 'Aqil (Lebanon) and the chronology of the Upper Paleolithic sequence in the Middle East. *Antiquity* **63**, 761–768.

McCown, T. D. & Keith, A. (1939). *The Stone Age of Mount Carmel. Vol. II*. Oxford: Clarendon University Press.

Molnar, S. & Molnar, I. M. (1985). The incidence of enamel hypoplasia among the Krapina Neandertals. *American Anthropologist* **87**, 536–549.

Neiburger, E. (1990). Enamel hypoplasias: Poor indicators of dietary stress. *American Journal of Physical Anthropology* **82**, 330–334.

Ogilvie, M. D., Curran, B. K. & Trinkaus, E. (1989). The incidence and patterning of dental enamel hypoplasias among the Neandertals. *American Journal of Physical Anthropology* **79**, 25–41.

Ortner, D. J. & Putschar, W. G. J. (1985). *Identification of Pathological Conditions in Human Skeletal Remains*. Smithsonian Contributions to Anthropology Number 28. Washington, DC: Smithsonian Institution Press.

Richard, G. D. & Anton, S. C. (1991). Craniofacial configuration and postcranial development of a hydrocephalic child (ca. 2500 BC–500 AD): With a review of cases and comment on diagnostic criteria. *American Journal of Physical Anthropology* **85**, 185–200.

Roberts, C. & Manchester, K. (1995). *The Archaeology of Disease*, 2nd ed. New York: Cornell University Press, pp. 41–43.

Roaf, R. (1960). Vertebral growth and its mechanical control. *J. Bone Joint Surg.* **42**, 40–59.

Saunders, S. R. (1992). Subadult skeletons and growth related studies. In (S. R. Saunders & M. A. Katzenberg, Eds.) *Skeletal Biology of Past Populations: Research Methods*. New York: Wiley-Liss, pp. 1–20.

Saunders, S. R. & Herring, A. A. (Eds.). (1995). *Grave Reflections: Portraying the Past through Cemetery Studies.* Toronto: Canadian Scholars Press.

Schwarcz, H., Grün, R., Vandermeersch, B., Bar-Yosef, O., Valladas, H. & Tchernov, E. (1988). ESR dates for the hominid burial site of Qafzeh in Israel. *Journal of Human Evolution* **17**, 733–737.

Sellier, P. (1995). Paléodémographie et archéologie funéraire: Les cimetières de Mehrgarh, Pakistan. *Paléorient* **21**, 123–143.

Skinner, M. (1996). Developmental stress in immature hominines from Late Pleistocene Eurasia: Evidence from enamel hypoplasia. *Journal of Archaeological Science* **23**, 833–852.

Smith, P., Bar-Yosef, O. & Sillen, A. (1984). Archaeological and skeletal evidence for dietary change during the Late Pleistocene/Early Holocene in the Levant. In (M. Cohen &

G. Armelagos, Eds.) *Paleopathology at the Origins of Agriculture*. Orlando, FL: Academic Press, pp. 101–136.

Sognnaes, R. F. (1956). Histological evidence of developmental lesions in teeth originating from Paleolithic, prehistoric and ancient man. *American Journal of Pathology* **32**, 547–577.

Taborin, Y. (2003). Le mer et les premiers hommes modernes. In (B. Vandermeersch, Ed.) *Echanges et Diffusion dans la Préhistoire Méditerranéenne*. Paris: CTHS, pp. 113–122.

Tchernov, E. (1984). Commensal animals and humans in the Middle East. In (J. Clutton-Brock & C. Grigson, Eds.) *Animals in Archaeology: Early Herders and their Flocks*. *Vol. 3*. BAR International Series 202. Oxford: British Archaeological Reports, pp. 91–115.

Tchernov, E. (1995). Biochronology, paleoecology, and dispersal events of hominids in the Southern Levant. In (T. Akazawa, K. Aoki & T. Kimura, Eds.) *The Evolution and Dispersal of Modern Humans in Asia*. Tokyo: Hokusen-Sha, pp. 149–188.

Tillier, A.-M. (1995). Paléoanthropologie et pratiques funéraires au Levant Méditerranéen durant le Paléolithique Moyen: Le cas des sujets non-adultes. *Paléorient* **21**, 6–76.

Tillier, A.-M. (1999). *Les Enfants Moustériens de Qafzeh. Interprétation Phylogénétique et Paléoauxologique*. Cahiers de Paléoanthropologie. Paris: CNRS Editions.

Tillier, A.-M., Arensburg, B. & Duday, H. (1989). La mandibule et les dents du Néanderthalien de Kébara (*Homo* 2), Mont Carmel, Israël. *Paléorient* **15**, 39–56.

Tillier, A.-M., Arensburg, B., Rak, Y. & Vandermeersch, B. (1988). Les sépultures Néanderthaliennes du Proche-Orient: Etat de la question. *Paléorient* **14**, 130–136.

Tillier, A.-M., Arensburg, B., Rak, Y. & Vandermeersch, B. (1995). Middle Paleolithic dental caries: New evidence from Kebara (Mount Carmel, Israel). *Journal of Human Evolution* **29**, 189–192.

Tillier, A.-M., Duday, H., Arensburg, B. & Vandermeersch, B. (2001). Brief communication: An early case of hydrocephalus: The Middle Paleolithic Qafzeh 12 child (Israel). *American Journal of Physical Anthropology* **114**, 166–170.

Tillier, A.-M., Kaffe, I., Arensburg, B. & Chech, M. (1997). An early case of hypodontia in the Middle East: Agenesis of lower premolar dated to ca. 92 ± 5 kyr at the Qafzeh Cave (Israel). *International Journal of Osteoarchaeology* **8**, 1–6.

Tillier, A.-M. & Tixier, J. (1991). Une molaire d'enfant Aurignacien à Ksar 'Aqil (Liban). *Paléorient* **17**, 89–93.

Trinkaus, E. (1983). *The Shanidar Neandertals*. New York: Academic Press.

Trinkaus, E., Smith, R. J. & Lebel, S. (2000). Dental caries in the Aubesier 5 Neandertal primary molar. *Journal of Archaeological Science* **27**, 1017–1021.

Vandermeersch, B. (1966). Découverte d'un objet en ocre avec traces d'utilisation dans le Moustérien de Qafzeh (Israël). *Bulletin de la Société Préhistorique Française* **66**, 157–158.

Vandermeersch, B. (1969). Les nouveaux squelettes Moustériens découverts à Qafzeh (Israël). *C. R. Acad. Sc. Paris* **268D**, 2562–2565.

Vandermeersch, B. (1970). Une sépulture Moustérienne avec offrandes découverte dans la grotte de Qafzeh. *C. R. Acad. Sc. Paris* **270D**, 298–301.

Vandermeersch, B. (1981). *Les Hommes Fossiles de Qafzeh (Israël).* Cahiers de Paléoanthropologie. Paris: Editions du CNRS.

Wapler, U. & Schultz, M. (1996). Une méthode de recherche histologique appliquée au materiel osseux archéologique: L'exemple des cribra orbitalia. *Bull. et Mém. Soc. Anthrop. Paris* **8**, 421–431.

Chapter XI

Hunting Pressure, Subsistence Intensification, and Demographic Change in the Levantine Late Middle Paleolithic

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Abstract

This paper examines the larger mammal faunal remains from the late Middle Paleolithic site of Kebara Cave, Mount Carmel, Israel, and offers four principal conclusions that can serve as working hypotheses in future research at Kebara and elsewhere in the Levantine Corridor. The first three of these conclusions relate specifically to the nature of hunting activities carried out at Kebara: (1) the hunters, on average, encountered fewer fallow deer than gazelle; (2) hunters traveled farther, on average, to procure gazelle than they did for fallow deer; and (3) hunting of both gazelle and fallow deer was highly seasonal and, for gazelle at least and probably also for fallow deer, took place mostly during the cooler months of the year. The fourth conclusion, like the first three, is directly relevant to understanding the nature of foraging activities that took place at Kebara, but it may also have broader evolutionary implications: (4) increasing hunting pressure, perhaps a consequence of growing human populations in the Levantine Corridor during the late Middle Paleolithic (after–60,000–55,000 years ago), led to a steady decline in red deer and aurochs and to greater use of juvenile and young adult gazelle, a trend of subsistence-related intensification that continued unabated into the early Upper Paleolithic.

Introduction

During the past two decades, archaeozoologists who work with Lower and Middle Paleolithic faunal assemblages have had to devote the lion's share of their efforts to taphonomic issues, developing ways to recognize and deal with patterning in their data that has little or nothing directly to do with human food-getting activities (e.g., Binford 1981, 1984, 1987; Klein 1987, 1989; see also Lyman 1994). At more or less the same time, the interesting idea that our premodern human ancestors, perhaps as recently as the Late Pleistocene, might have been scavengers, not hunters, of larger mammals also absorbed a great deal of our intellectual energy (e.g., Binford 1984). Resolving this issue required new models and new tools to help us discriminate between animals that had been killed by non-human predators from those taken by hunters. While the hunter-scavenger debate, most certainly as it applies to the latter part of the Pleistocene, is now largely behind us, it nevertheless was a stimulating and productive step in the development of contemporary archaeozoology as a discipline.

We have clearly learned a great deal from these endeavors, and the field of archaeozoology has been greatly enriched in the process, but not without some cost. While we are now much better equipped to recognize the signatures of human involvement in the formation of Lower and Middle Paleolithic faunal assemblages, and most are agreed that large-mammal hunting was a *bona fide* part of human foraging strategies for at least the last 200,000 years, and probably much longer (e.g., Stiner 2002; Gaudzinski & Roebroeks 2000), until fairly recently there have been very few fine-grained studies of what these archaic human hunters actually did. Fortunately, this situation is now changing rapidly, as archaeozoologists increasingly are able to move beyond the necessary taphonomic "preamble" and begin to probe their data for insights into the hunting behavior of pre-modern human foragers. Nowhere has this change been more apparent than in the study of Middle Paleolithic faunal assemblages. There are now many studies that explore the hunting strategies of Neanderthals, examining many facets of their use of animal resources from the initial stages of procurement, field processing, and transport to consumption and final discard (e.g., Auguste 1992; Baryshnikov et al. 1996; Blasco et al. 1996; Boyle 1998; Brugal et al. 1998; Burke 2000; Chase 1986, 1988; Conard & Prindiville 2000; Díez et al. 1999; Farizy et al. 1994; Gaudzinski 1995, 1996; Gaudzinski & Roebroeks 2000; Grayson et al. 2001; Hoffecker & Cleghorn 2000; Jaubert et al. 1990; Klein 1999, and references therein; Marean & Kim 1998; Patou-Mathis 2000; Speth & Tchernov 1998, 2001, 2002; Stiner 1994; Stiner et al. 1999; Stiner & Tchernov 1998; Tortosa et al. 2002; Valensi 2000; Villaverde et al. 1996). The present paper seeks to contribute in some small measure to this rapidly growing corpus of case studies, adding specifically to the information available for the late Middle Paleolithic in the Levantine Corridor area. Focusing on gazelle and fallow deer, the dominant larger mammal taxa at Kebara, I examine three specific aspects of the hunting behavior of the site's Neanderthal inhabitants: (1) average transport distance from kill to cave, (2) seasonal timing of procurement activities, and (3) hunting pressure on the largest prey types. Before delving into these issues, however, I begin with a very condensed discussion of the site and the methods used in studying the faunal remains; for a more detailed discussion of these matters, see Bar-Yosef et al. (1992) and Speth & Tchernov (1998, 2001).

Background and methods

Kebara is a large cave on the western face of Mount Carmel (Israel), about 30 km south of Haifa and 2.5 km east of the present-day Mediterranean shoreline (Figure 1). Two major excavations at the site, the first conducted by Moshe Stekelis between 1951 and 1965 (Schick & Stekelis 1977) and the second by a French-Israeli team co-directed by Ofer Bar-Yosef and Bernard Vandermeersch between 1982 and 1990 (Bar-Yosef 1991; Bar-Yosef et al. 1992), yielded hundreds of thousands of animal bones and stone tools from a four-meter deep sequence of late Middle Paleolithic deposits dating between approximately 60,000 and 48,000 years ago (Valladas et al. 1987).

Stekelis's excavations were conducted within 2 x 2-m grid squares using arbitrary horizontal levels (spits), typically 10 cm in thickness, although many were thicker. Almost all of the excavated deposits were screened and virtually all faunal remains, including thousands of unidentifiable bone fragments, were kept. Depths for levels were recorded in cm below a fixed datum. In the more recent work at the site, the excavators employed 1-m grid units (often divided into four 50 x 50-cm quadrants), many items (including fauna) were piece-plotted, and wherever possible they followed the natural stratigraphy of the deposits, using levels that seldom exceeded 5 cm in thickness. Depths were again recorded in cm below datum, using the same reference point that Stekelis had used. The newer excavations recognized nine natural stratigraphic levels (units or "couches") within the Mousterian sequence: unit XIII (bottom) to unit V (top). The early Upper Paleolithic levels begin with unit IV. While both approaches – arbitrary horizontal spits and natural stratigraphic levels – result in the pooling of material from more than one occupational episode, for issues concerning change over time I focus heavily on materials from the newer excavations in order to minimize the distortion that may arise from the use of aggregated samples. For other issues, in which the Middle Paleolithic can be treated as a single entity, the Stekelis materials are also included, vastly enlarging the sample sizes.

At least 10 different taxa of larger mammal were exploited by Kebara's Middle Paleolithic inhabitants, including gazelle, three species of cervid (roe deer, fallow deer, and red deer), aurochs, two or more equids, wild boar, wild goat, and perhaps even rare hartebeest. A few bones and teeth of rhinoceros are also present, but their taphonomic history has not yet been investigated. Among

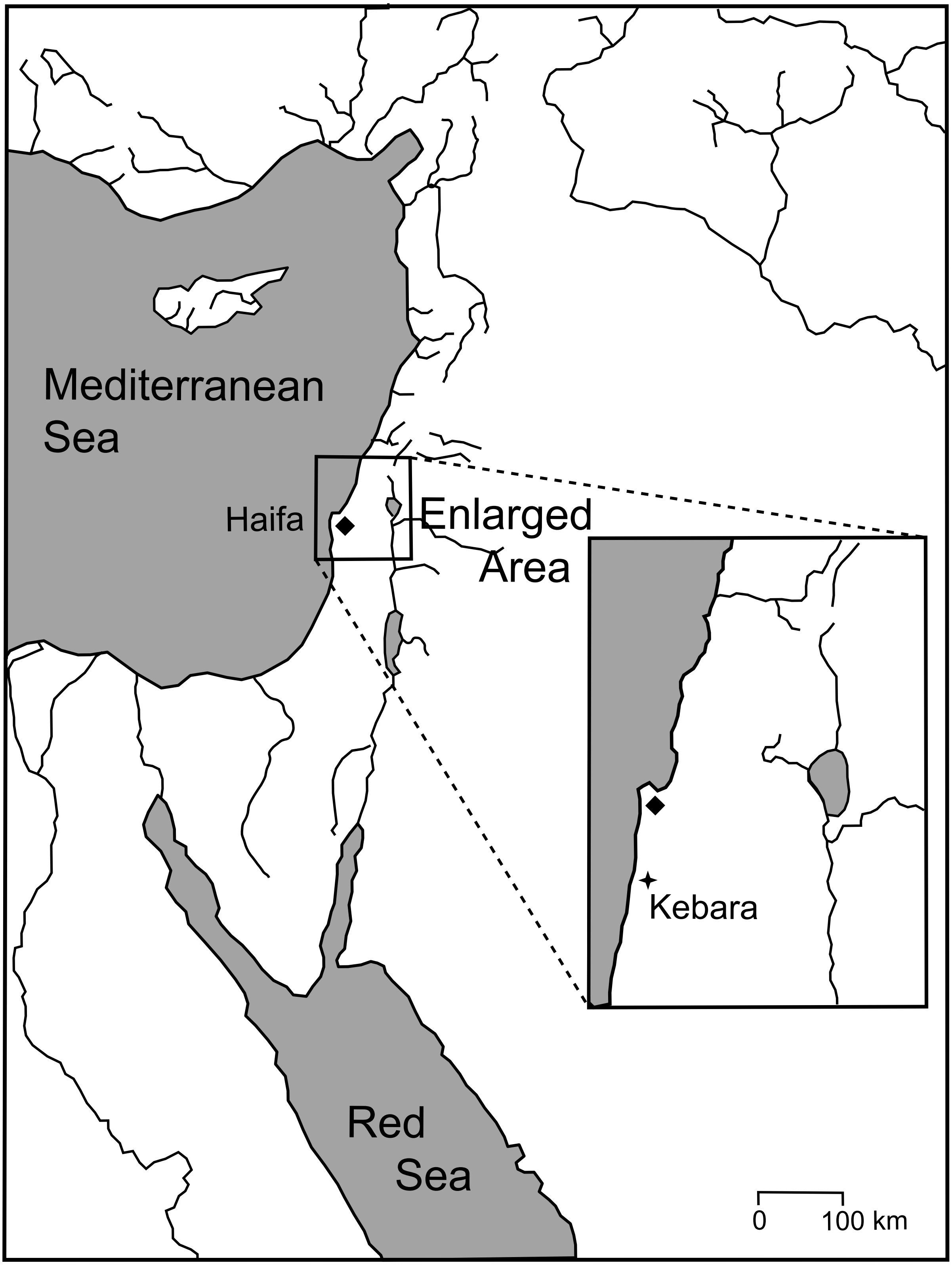
Mediterranean Sea
Haifa
Enlarged Area
Kebara
Red Sea
0
100 km

Figure 1. Location of Kebara Cave in the Southern Levant.

the many taxa, two overwhelmingly dominate the assemblages throughout the Middle Paleolithic sequence – mountain gazelle (*Gazella gazella*) and Persian fallow deer (*Dama mesopotamica*). Together, these two ungulates make up over 80% (NISP) of the larger mammals (Figure 2). The discussion that follows, therefore, focuses primarily on gazelle and fallow deer, in part because these taxa are such a prominent part of the fauna, and in part simply because the sample sizes for the other taxa are insufficient to allow statistical treatment.

While there is clear evidence throughout the Middle and Upper Paleolithic sequence for the intermittent presence of carnivores, most notably spotted hyenas (*Crocuta crocuta*), the modest numbers of gnawed and punctured bones, the scarcity of gnaw-marks on midshaft fragments (Marean & Kim 1998:S84–S85), and the hundreds of cutmarked and burned bones, as well as hearths, ash lenses, and large numbers of lithic artifacts, clearly testify to the central role played by humans in the formation of the bone accumulations (see Bar-Yosef et al. 1992 and Speth & Tchernov 1998, 2001 for more detailed treatment of taphonomic issues).

Throughout this paper, NISP (number of identifiable specimens) indicates the number of bones and teeth that could be assigned to a particular taxon (e.g., *Gazella*), but it also includes those fragments that could not be identified to a taxon but were evidently from animals of similar body size (e.g., gazelle-sized). MNI (minimum number of individuals) is the estimate of the minimum number of animals that would have been killed to produce a given NISP value. The MNI for a given taxon is based on the element, portion, age, and side that yields the largest number of individual animals (e.g., left fused distal tibia or right permanent lower third molar). The ratio of total NISP to MNI of a particular taxon (ΣNISP/MNI) is used as a crude approximation of relative skeletal completeness (i.e.,

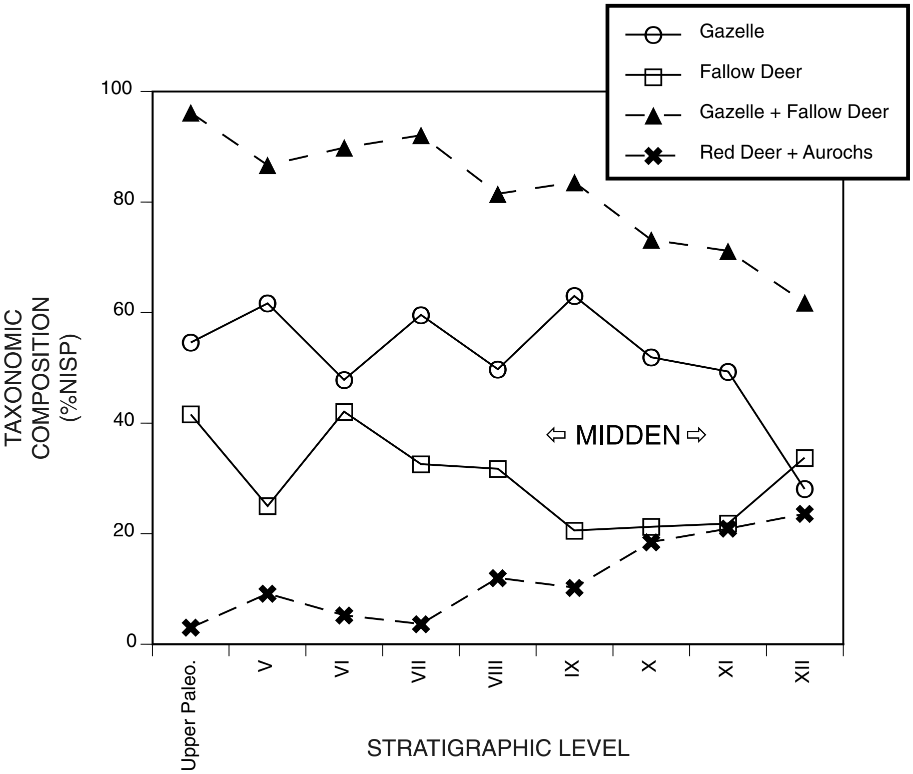

Figure 2. Proportion of gazelle and fallow deer among the larger mammals at Kebara Cave (%NISP, calculated on the basis of NISP values for 7 taxa – *Bos*, *Capra*, *Cervus*, *Dama*, total equids, *Gazella*, and *Sus*; total NISP=14,962).

higher values of the ratio denote more complete skeletons).

I evaluate results statistically using the following methods: arcsine transformation (t_s), as defined by Sokal & Rohlf (1969:607–610), for testing the significance of the difference between two percentages; and the standard unpaired t-test (t) and F-test for evaluating differences between means and variances, respectively.

Average transport distance

Modern mountain gazelle are smaller than Persian fallow deer (gazelle: female, 16–18 kg; male, 20–25 kg; fallow deer: female, ca. 80 kg; male, ca. 100 kg; Baharav 1974:42; Chapman & Chapman 1975; Frankenberg 1992:355; Haltenorth 1959; Horwitz et al. 1990; Mendelssohn & Yom-Tov 1987). Nevertheless, on the basis of ethnographic observations among modern hunter-gatherers, both animals are small enough to have been treated in broadly similar ways with regard to transport decisions based just on body size (i.e., gazelle and fallow deer fall into size classes 1 and 2, respectively, as defined by Bunn 1991:442; see also O'Connell et al. 1988, 1990 for more detailed discussions of transport decisions in relation to prey body size and other factors). Thus, other things being equal (such as the average size of available transport parties), any major contrast between the two taxa in body-part representation is most likely to reflect differences in the average distance that the carcasses had to be transported from the locus of the kill to the cave. And as Figure 3 shows, clear-cut differences in body-part representation are, in fact, evident at Kebara. Thus, particularly during the so-called "midden period" (units IX–XI), the degree of skeletal completeness, as crudely approximated by the ratio of ∑NISP/MNI, is substantially greater in fallow deer than in gazelles, implying that wooded habitat suitable for

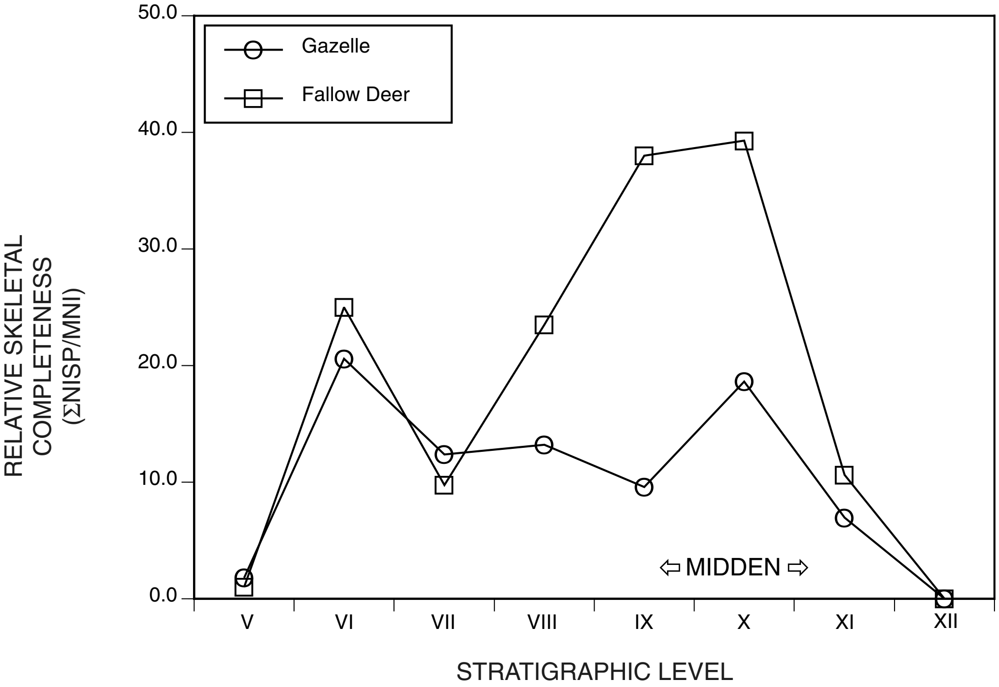

Figure 3. Relative skeletal completeness of gazelle and fallow deer as approximated by the ratio of ∑NISP/MNI.

hunting deer was available closer to the cave than more open terrain where gazelles are more likely to have been procured (for a discussion of the evidence for midden development in Kebara during the late Middle Paleolithic, see Speth & Tchernov 2001).

This conclusion is reinforced by other lines of evidence. For example, average overall utility, as approximated by Binford's (1978) Modified General Utility Index or MGUI, is slightly but significantly lower in fallow deer than in gazelle, very likely a reflection of the presence of a broader range of low- to moderate-utility skeletal elements, as might be expected if more complete carcasses were brought into the cave ($t = 3.82$, $p = .0001$).

The limb elements reveal a similar story. In deer, front and rear limb units are about equally well represented (front limb, 49.4%; hind limb, 50.6%), whereas in gazelle there is a greater emphasis on the higher-utility elements of the rear limb (front limb, 38.8%; hind limb, 61.2%); these proportions differ significantly between the two taxa ($t_s = 5.77$, $p < .0001$). The low-utility elements of the feet reveal the same pattern. Deer phalanges are slightly but significantly better represented (26.5%) than the foot bones of gazelle (23.2%; $t_s = 3.26$, $p = .001$). Such selective culling in a comparatively small animal suggests transport from a fairly considerable distance.

The immature remains may also suggest that deer were being taken closer to Kebara than gazelle. Using the frequencies of lower and upper fourth premolars and third molars (i.e., dP_4, dP^4, P_4, P^4, M_3, and M^3) as the most reliable data for determining the age structure of the Kebara ungulates, and assuming that immature animals generally are less desirable targets than adults (see discussion in Speth 1983), significantly fewer immature gazelle (16.3%) reached the cave than juvenile fallow deer (30.3%; $t_s = 6.06$, $p < .001$), implying that the gazelle were being taken farther from the site. Obviously, factors other than transport distance, such as differences in the age structure of the herds, as well as the seasonal timing of the hunts, the method of procurement, and of course taphonomic biases, can influence the proportion of juveniles in a hunted assemblage. Thus, by itself, a higher proportion of immatures among the fallow deer is not particularly compelling evidence that the herds were generally encountered closer to the cave (I return again to the issue of immatures below). However, another somewhat more convincing piece of evidence points in the same direction: the average utility (MGUI) of the juvenile postcranial remains (i.e., elements with unfused or fusing epiphyses) is lower in deer (29.2) than in gazelle (35.7; $t = 2.81$, $p = .005$; MGUI from Binford 1978:74). As before, the lower average utility of the immature deer remains implies that more complete carcasses of these animals were brought into the cave.

Seasonality

Procurement of both gazelle and fallow deer appears to have been highly seasonal. This is shown by histograms of crown-height measurements for the lower (or mandibular) M_3. In both gazelle (Figure 4) and fallow deer (Figure 5), the histograms are strikingly multi-modal, each with three

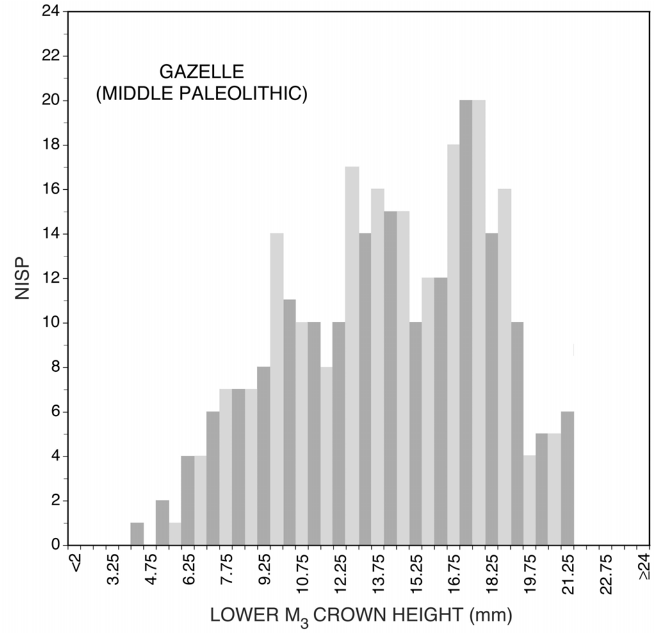

Figure 4. Crown-height measurements (mm) for lower third molars (M_3) of gazelle.

principal peaks. Unfortunately, we lack sufficient information on the relationship between wear rate and age in either of these animals to assign the modes to a specific season of the year, but at the very least we can say that the peaks very likely reflect annual age classes. According to Davis (1994:87), the M_3 in gazelle is fully formed at about 8 months and erupts at approximately 12 months. This means that the unerupted teeth in Figure 4 (i.e., those with crown heights in excess of about 20 mm) are from fawns, and those in the first major mode (i.e., with crown heights clustering around 17–18 mm) are very likely yearlings (I follow Dunham 1997:207 in classifying males between 1 and 2 years of age as yearlings and females in this same age cohort as young adults). From these results, and given the fact that nearly 70% of the sexed gazelle skeletal elements are female (based on morphological characteristics of the pubis and dimorphism in horn cores), it would appear that most of the gazelle killed by Kebara's hunters were quite young. As additional faunal data become available from other Middle Paleolithic sites in the Levant, it will be interesting to see whether the heavy focus on juvenile and young adult female gazelle (and probably fallow deer as well) is unique to Kebara or instead represents a region-wide phenomenon in the late Middle Paleolithic; it will also be interesting to see whether this hunting pattern is less apparent earlier in the Middle Paleolithic (see discussion below).

We can approximate the season of gazelle procurement somewhat more precisely by focusing on the crown-height measurements of the lower deciduous fourth premolar or dP_4 (Figure 6). Unworn dP_4s denote unborn or newborn animals (up to about 1 month old; Davis 1983:57). According to Davis (1983:57, 1987:79), these teeth generally wear down until only about 2–3 mm of crown remains, and by 13–15 months they are shed as the permanent P_4 erupts. Klein & Cruz-Uribe (1984:46–49), expanding on a method developed by Spinage (1971, 1973, 1976), advocate estimating an animal's age at death using a non-linear or quadratic model of crown-height wear. This approach is based upon the view that crown height

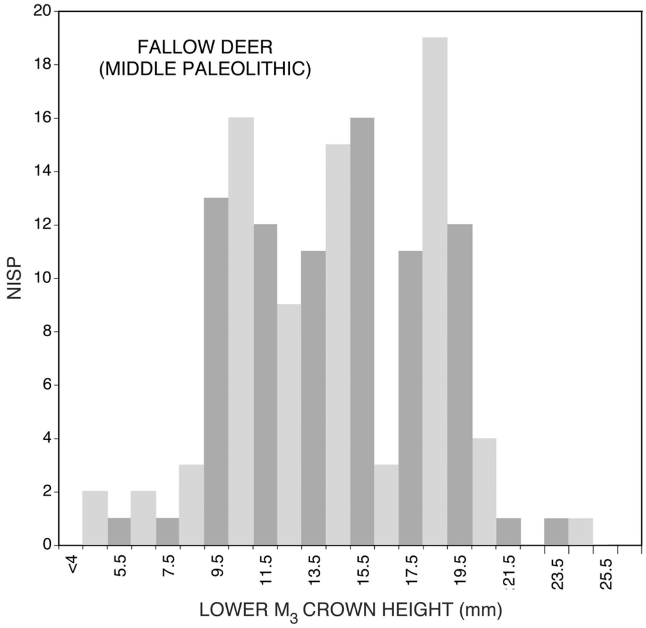

Figure 5. Crown-height measurements (mm) for lower third molars (M_3) of fallow deer.

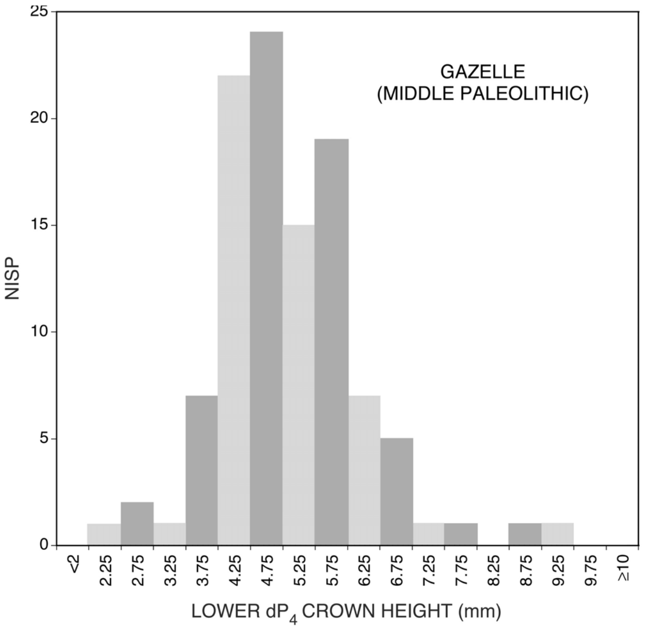

Figure 6. Crown-height measurements (mm) for deciduous lower fourth premolars (dP_4) of gazelle (NISP=107).

does not decrease linearly with age, but is most rapid when the tooth is only slightly worn, and proceeds more slowly as the occlusal surface becomes broader and flatter. Gifford-Gonzalez (1991), however, offers contradictory evidence, suggesting that, in at least bison and sheep, teeth may wear slowly in the early stages. We presently lack data for gazelle that would allow us to determine which approach provides more realistic age estimates for this species. Fortunately, however, Davis (1983:61, 1987:80) has published crown-height values for the dP_4s of 18 juvenile animals of known age at death housed in collections at the Hebrew University of Jerusalem. Using Davis' regression equation ($y = 7.74 - 0.229x$; where y is the crown height in mm and x is the age in months), the mean age of juvenile gazelle from the midden (units XI–IX) is 12.6 months (mean crown height, 4.85 mm). When all of the data from the Stekelis and more recent excavations are pooled to maximize the sample size, the regression yields a slightly younger estimate of 11.8 months (mean crown height, 5.03 mm).

Despite the apparent precision of the results, they must be regarded as very approximate at best. First, Davis' modern sample of known-age individuals is small (N=18), and the fit between age and crown height displays substantial scatter around the regression line. There is even a hint in his data that the teeth of the youngest individuals wore faster than the older ones, as might be expected by the quadratic model. Unfortunately, there are only three individuals at the young end of the sample, making any attempt at a firmer conclusion unwarranted. Other reservations about the Kebara results should also be noted. For example, we know that modern gazelle are smaller than their Late Pleistocene predecessors (Davis 1987:69), and the abrasiveness of their diet today may also be different from that of animals living during the Middle Paleolithic. It is not unreasonable, therefore, to expect that the relationship between age and crown height might differ as well. Finally, the use of dental wear as a means of estimating season of death assumes that animals were all born during a single fairly tightly constrained birthing or calving season, ignoring the fact that modern Israeli gazelles actually display two distinct peaks, the principal one in the spring and a second, minor one in the fall (Baharav 1983:447). The crown-height approach also ignores the likelihood that at least some births occurred out of season (Baharav 1983:447), and makes the even more tenuous assumption that the birth season was the same during the Late Pleistocene as it is today. Granted that Israel was not glaciated during the Middle Paleolithic, and granted also that the length of the photoperiod, which plays an important role in fixing the timing of the birth season in many taxa (e.g., Lincoln 1992; Loudon & Brinklow 1992), has remained unchanged, nevertheless the fluctuations in both temperature and rainfall documented in the Soreq oxygen-isotope record make it quite possible that the timing of the peak in births may have been somewhat different in the past than it is today (see Bar-Matthews et al. 1998, 1999). So, looking at the results with these rather daunting caveats in mind, we should not push the precision of our interpretation beyond the suggestion that most of the Kebara juveniles, at least those killed during the unit IX–XI midden period which comprise the bulk of the sample, were probably taken in the late winter or spring, that is, roughly a year, give or take a few months, after the principal birth peak which, today at least, occurs in April (see discussion and references in Speth & Tchernov 2001:58).

There is even a hint in the dental data that the seasonal timing of gazelle hunts may have been somewhat more constrained than hunts for deer. This is suggested by the observation that the ages of the immature gazelle, as assessed by crown-height measurements for the lower and upper deciduous fourth premolars, are significantly less variable than the ages of the immature deer (dP_4, F-Value = 0.61, $p = .06$; dP^4, F-Value = 0.29, $p = .0001$; see Table 1). This conclusion holds, however, only if one is willing to accept the somewhat dubious assumption that the difference between these two taxa in the pattern of crown-height variability is largely reflective of differences in age structure rather than fundamental differences in wear trajectories stemming from their contrasting diets and radically differing tooth size, shape, and structure.

Table 1. Crown-height values (mm) for lower (dP_4) and upper (dP^4) deciduous fourth premolars of gazelle and fallow deer.

	dP_4			dP^4		
Species	N	Mean ± 1 SD	Variance	N	Mean ± 1 SD	Variance
Gazelle	107	5.03 ± 1.09	1.19	45	6.36 ± 0.86	0.73
Fallow Deer	41	6.91 ± 1.39	1.94	38	7.17 ± 1.59	2.53

Hunting pressure

One of the most striking features of Kebara's faunal record is the monotonic decline of the principal larger-bodied animals – red deer and aurochs – over the entire four-meter-long late Middle Paleolithic sequence, a trend that continues into the early Upper Paleolithic (see Figure 2 above). Particularly noteworthy is the fact that this decline continues unabated across several major swings in regional paleoclimate that are clearly evident in the speleothem-based oxygen-isotope record from Soreq Cave in Israel (see Figure 7; data from Bar-Matthews et al. 1998, 1999; see also Speth & Tchernov 2002). It should be noted that the isotope data shown in Figure 7 have been "smoothed" using a cubic spline statistical averaging procedure. This technique estimates an average value for *y* using four values of *x* at a time (i.e., fixed window width).

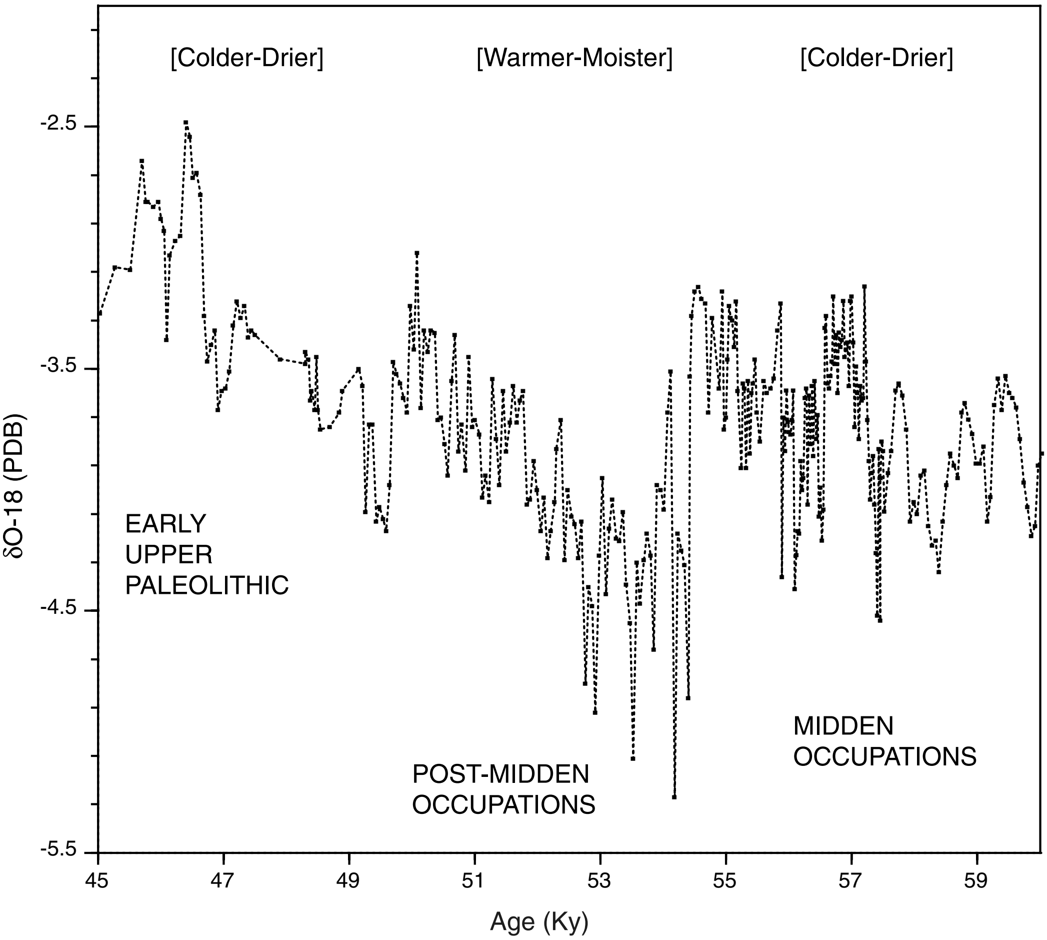

Figure 7. Smoothed oxygen-isotope record ($\delta^{18}O$ ‰ PDB), derived from speleothems in Soreq Cave (Israel), for the period – 60,000–45,000 years ago. Original data provided by M. Bar-Matthews (see Bar-Matthews et al. 1999:88, their Figure 1A for unsmoothed record).

The program uses "...a series of cubic (third-order) polynomials to fit a moving window of data, four points at a time" (SAS Institute Inc., 1998:227). This smoothing procedure eliminates many of the minor oscillations in the data, thereby allowing one to more readily perceive the major trends. According to the Soreq record, $\delta^{18}O$ values were generally lower between roughly 54,000 and 48,000 years ago, denoting a shift toward somewhat warmer-moister conditions. Chronologically, this correlates (approximately) to Kebara's units VI and VII (Valladas et al. 1987). This interval is bracketed on either side by periods of generally higher $\delta^{18}O$ values indicative of colder-drier conditions corresponding, at least approximately, to the "midden period" of units IX–XI and the terminal Middle Paleolithic (unit V) and early Upper Paleolithic (unit IV) levels.

In light of the Soreq record, it seems very unlikely that the "phasing out" of the two largest-bodied taxa can be attributed in any simple or direct way to changes in paleoclimate. Instead, increasing predator pressure seems a more likely cause, the predator of course being the Neanderthal inhabitants of the region (see Davis et al. 1988 for an early discussion of this possibility). Obviously, such an idea would have seemed preposterous only a decade or so ago when many prehistorians, myself included, subscribed to the view that Neanderthals, and other archaic forms of *Homo sapiens*, were opportunistic scavengers of larger game (e.g., Binford 1984, 1988). But as we increasingly come to accept that these archaic humans were in fact effective and highly successful hunters, the possibility that they might have over-exploited the larger taxa in a region can no longer be rejected outright (e.g., Boëda et al. 1999; Milo 1998; Stiner 1994, 2002; Speth & Tchernov 1998; Thieme 1997). Of course, merely granting that Levantine Neanderthals were capable of bringing down prime-adult aurochs and red deer in no way means that they drove these animals to near-extinction. Most paleoanthropologists seem to assume, for the most part implicitly, that pre-modern human population densities in the eastern Mediterranean would have been far too sparse to have had such an impact on these animals. However, Stiner et al. (1999, 2000) recently presented tantalizing, albeit tentative, evidence, based on declining mean body sizes of Late Pleistocene tortoises, that human populations in the Levant may, in fact, have grown considerably toward the end of the Middle Paleolithic, after about 55,000 years ago, thereby reopening the door to discussions of Neanderthal hunting pressure on the larger ungulates. Unfortunately, we still know discouragingly little about Neanderthal demographics in the region. Thus, at the moment we still have no firm basis for either affirming or rejecting the idea that hunting pressure, perhaps in conjunction with paleoenvironmental changes, contributed to the decline of the larger-bodied taxa. However, the apparent independence of this decline from major swings in the paleoclimatic record certainly makes over-hunting a prime candidate, one that warrants much more thorough exploration.

Kebara provides a few other pieces of evidence, albeit tentative ones, that may also point to over-hunting in the latter part of the Middle Paleolithic. Perhaps the most compelling of these is provided by the juvenile remains. The proportion of immature gazelle (%NISP) in the assemblage, based on the numbers of unfused or fusing epiphyses, increases from an average of about 7% in the midden levels to 11% in the upper part of the sequence and to 15% in the early Upper Paleolithic (Figure 8), quite possibly a reflection of increasing hunting pressure on local herds. Unfortunately, when we use only the faunal remains that were recovered according to natural stratigraphic levels, as in Figure 8, the sample sizes are very small and the differences are not statistically significant. However, if we also include the Stekelis materials and arbitrarily split the Middle Paleolithic sequence at 650 cm below datum, a crude approximation of the boundary between the principal period of midden formation and the overlying post-midden levels, not only is the increase in juveniles still clearly visible, but the differences now achieve significance (midden levels, 10.2%; post-midden levels, 12.9%; $t_s = 2.10$, $p < .05$). The early Upper Paleolithic sample remains small, however, and the proportion of juveniles (15.2%) does not differ statistically from the value

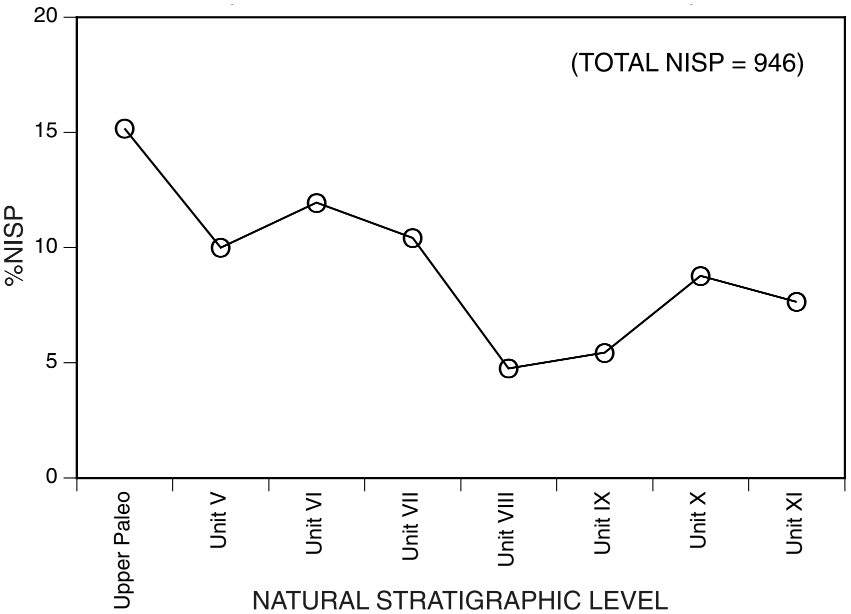

Figure 8. Proportion of juvenile gazelle (%NISP) at Kebara, based on the frequency of unfused and fusing epiphyses.

in the post-midden levels ($t_s = 1.61, p > .05$). However, when it is compared to the midden levels beneath, the difference is highly significant ($t_s = 3.35, p < .01$).

Unfortunately, while the increase in the proportion of juveniles is clear, the meaning of this change is less so. I have argued elsewhere that the younger Mousterian assemblages at Kebara may reflect hunting activities that took place primarily during the warmer months of the year, whereas midden-period hunting was more heavily concentrated during the cooler months of late winter or spring (Speth & Tchernov 2001). These seasonality determinations were based largely on changes over the course of the sequence in the sex ratios of both gazelle and fallow deer. Thus, it is conceivable that hunters simply encountered more young animals during the later occupations and hence brought more immature carcasses back to the cave. However, if one accepts the view that juveniles typically are much lower ranked as prey than their adult counterparts, both because of their smaller size and because of their small lipid reserves, then the increase in juveniles at Kebara reflects not a higher rate of encounter of young animals but a decline in encounters of preferred age classes, and hence a sign of increasing diet breadth or "intensification" (see Speth 1983).

While data on the fusion state of epiphyses allow us to monitor changes in the number of immature gazelle, they provide no insights into the proportions of prime versus old adult animals. To see if the composition of the adult component of the assemblage also underwent significant change during the late Middle Paleolithic, we have to turn to the teeth. For this we follow procedures broadly similar to those used by Stiner (1994:288–292) in her study of Italian Middle Paleolithic faunas, though we maximize the number of specimens in our study by employing not only the fourth premolars but also the third molars, and we use teeth from both mandible and maxilla. Like Stiner, we divide the teeth into three broad age classes – juvenile, prime adult, and old adult. Juveniles are represented by the deciduous premolars as well as unerupted third molars; adults are represented by the permanent teeth, with the boundary between prime and old adult animals placed at the point when approximately half of the tooth crown has been worn away. As we have already seen, juveniles increase by about 4% from the midden levels to the post-midden levels. Because of closure, the fact that the total of a series of percentages must add up to 100%, the rise in juveniles has to be accompanied by a decline in at least one of the other age classes. Interestingly, what declines is the proportion of old adults, not prime adults, and the drop, though small, is significant (from 16.7% to 12.6%, $t_s = 1.96$, $p = .05$). This result is consistent with a scenario of over-hunting.

This shift toward younger individuals *among the adults* can be illustrated in another way that brings out the trend far more clearly. In Figure 9, mean crown heights for the lower or mandibular third molar (M_3) of *adult* deer and gazelle are plotted by arbitrary one-meter thick levels. This figure shows that mean crown heights in adult gazelle increase steadily from the beginning of the sequence right into the early Upper Paleolithic, while there is no discernible trend in the values for adult fallow deer. The implication of Figure 9 is that, over time, Kebara's Neanderthal hunters focused ever more heavily on younger adult gazelle, a reasonably clear sign of subsistence intensification.

Interestingly, while the fusion and dental data point to increasing use of juvenile and young adult gazelle, prey that would have been ranked lower than their prime adult counterparts, other data suggest that the hunters had to travel farther to do so, further indication of subsistence intensification during the latter part of the Middle Paleolithic. Several lines of evidence point to this conclusion. For example, in the midden period the proportion of rear limbs is similar in both gazelle (57.0%) and deer (54.1%; $t_s = 0.99$, $p > .05$). However, in the post-midden levels rear limbs of gazelle increase to 63.8%, a change that is highly significant ($t_s = 3.27$, $p = .001$), whereas in deer they remain essentially unchanged (48.5%; $t_s = 1.80$, $p > .05$). Greater selective culling of the lower-utility elements of the front limb in the post-midden period implies longer average transport distances.

The frequency of heads relative to other body parts

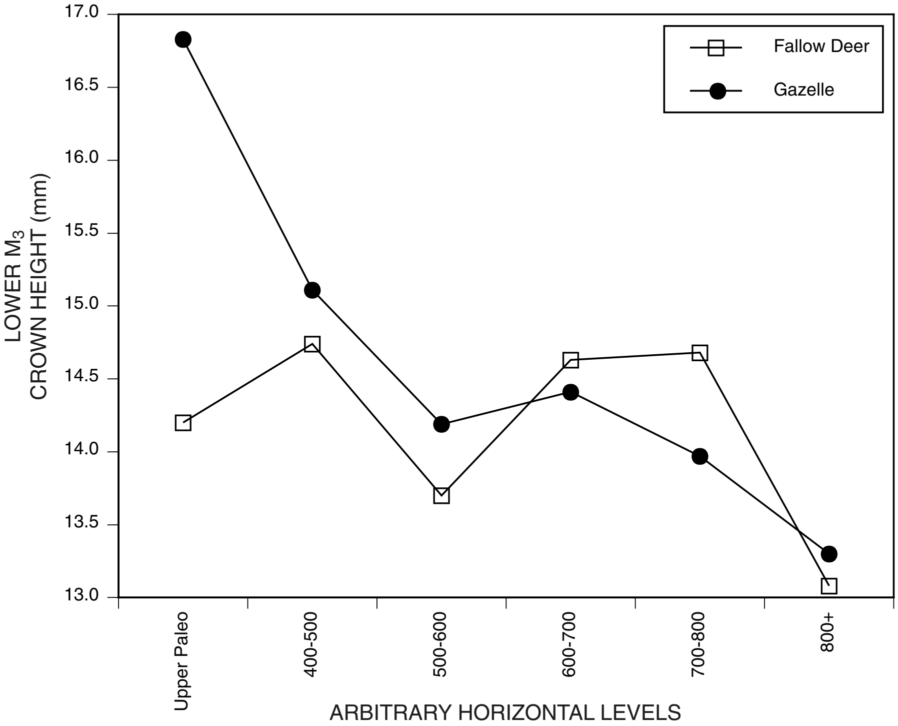

Figure 9. Mean crown height values of *adult* deer (NISP=191) and gazelle (NISP=404) lower third molars (M_3) plotted by arbitrary one-meter-thick levels.

provides another useful index of transport distance, the underlying assumption being that if an animal's head is to be transported at all, then for a given body size the greater the distance from kill to basecamp the lower the likelihood that the head will be moved. In the midden levels, the proportion of heads is somewhat greater in gazelle (47.5%) than in fallow deer (43.0%; $t_s = 3.06$, $p < .01$), very likely a reflection of the smaller body size of gazelle. However, in the post-midden levels, gazelle heads drop to 39.8% ($t_s = 6.87$, $p < .0001$), while deer heads remain essentially unchanged (42.4%; $t_s = 0.38$, $p > .05$). The implication is that in the latter part of the Middle Paleolithic the average distance to deer remained more or less unchanged, whereas hunters had to travel farther to reach the gazelle herds.

The average marrow utility of the gazelle limb elements, again using the pooled assemblage to maximize sample sizes, points to the same conclusion (Binford 1978). I use marrow rather than general utility here because most of the limb bones would have been transported first and foremost for their marrow yield. Deer remains show no significant change in average marrow utility from the midden (55.5) to the post-midden period (55.2, $t = 0.14$, $p > .05$). In contrast, the average marrow utility for gazelle limb elements in the midden levels is 53.0 rising to 57.2 in the younger levels ($t = 3.11$, $p < .01$). If increasing average utility indicates that a narrower range of moderate- to high-utility elements were brought to the cave, we are again seeing evidence for greater average transport distance to acquire prey of steadily declining resource value.

Conclusions

The patterning that I have discussed here points to four interesting conclusions: (1) Kebara's Neanderthal hunters, on average, encountered fewer fallow deer than gazelle; (2) hunters generally had to travel farther to procure gazelle than they did for fallow deer; (3) hunting of both gazelle and fallow deer was a highly seasonal activity and, for gazelle at least and probably also for deer, most hunts took place during the cooler months of the year; and (4) increasing hunting pressure over the course of the late Middle Paleolithic, probably in response to locally increasing human populations, perhaps a reflection of regionally growing human populations, led to a steady decline in red deer and aurochs and increasing use of both immature and young adult gazelle, a trend of subsistence-related intensification that continued unabated into the early Upper Paleolithic.

The patterning that points to over-hunting in the late Middle Paleolithic at Kebara is reasonably robust and clear. But I have made no attempt here to show that this trend affected the Levantine Corridor as a whole, and further work elsewhere in the Levant could, in fact, show that it occurred only at Kebara and not farther afield. Fortunately, this is a potentially tractable matter that can be addressed through more regionally focused comparative studies of Middle Paleolithic faunas. This will not be an easy or straightforward task, however, as many different factors can intervene to complicate matters. For example, even if over-hunting were, in fact, occurring throughout the region, the impact of such intensified hunting practices may not become evident everywhere at the same time or to the same extent. In addition, depletion of large-game resources at the regional scale may be difficult to see if the sites that are being compared were occupied at different seasons of the year, and especially if the occupations represent different functional poses within their respective settlement systems (e.g., basecamp vs. short-term hunting station). Differences in site function may become particularly problematic if comparisons are made between open-air hunting locations close to fixed watering points where large game could be predictably ambushed, and basecamp occupations in caves such as Kebara to which game was transported. Ethnographic studies among the Hadza and Bushmen demonstrate quite strikingly that remains of large game are likely to be over-represented in the open-air ambush localities, while small game will be more heavily in evidence in the cave sites (e.g., Brooks 1996; O'Connell et al. 1988, 1990).

More importantly, merely recognizing such patterning at Kebara is a far cry from explaining it, and my attempt at explanation here should be regarded as a very preliminary working hypothesis, not as a conclusion to which I am deeply wedded. We constantly face the problem of equifinality, of seeing a fit between an idea and the data, and concluding on that basis that we have shown the correctness of the idea (in the misleading parlance of contemporary archaeology, "confirming our hypothesis"). In reality, of course, we have not actually proven anything, we have simply failed to falsify the hypothesis. I also regard parsimony – giving priority to the simplest explanation – not as a fact of the way nature works but as a reflection of our frequent inability to grasp and deal with the complexity of the real world. Put another way, I operate with the underlying expectation that the "right" answer, or at least the most productive avenue to pursue, is likely to be one that we have not even thought of as yet, one that often turns out to be quite counterintuitive in terms of what we assume to be correct at the moment.

But I do not believe that all of this is an exercise in futility either. If we eliminate dead ends and raise new questions, the whole enterprise does move forward. In terms of the issues that are of concern here, at stake is our understanding of the basic "humanness" of Neanderthals or Neanderthal-like hominids. In what ways were they like us, and in what ways were they different? And, more importantly, are these differences a reflection of a fundamental, biologically based cognitive chasm that separates "them" from "us," as scholars such as Klein (2003) and Stringer & McKie (1997) believe to be the case, or are we instead seeing differences that merely reflect the gradual unfolding – the "intensification," if you like – of demographic, technological, and socioeconomic processes in populations of ancient humans who were operating with more or less the same mental hardware as we do (e.g., Hayden 1993)? I obviously favor the latter perspective, and the direction this paper has taken clearly reflects this. But I also maintain my deep-seated apprehensions about equifinality, about all too easily concluding that we are right just because our limited data appear to fit what are almost certainly naive expectations of the day. So I have identified patterning and, to the extent possible, I have suggested what seems to be a plausible direction for explanation, but I do so with the understanding that my conclusions are not firm but working hypotheses, whose primary value is to focus attention on issues that are worth exploring further. Alas, tomorrow much of this will almost certainly need to be rewritten....

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References

Auguste, P. (1992). Etude archéozoologue des grands mammifères du site Pléistocène Moyen de Biache-Saint-Vaast (Pas-de-Calais, France): Apports biostratigraphiques et palethnographiques. *L'Anthropologie (Paris)* **96**, 49–70.

Baharav, D. (1974). Notes on the population structure and biomass of the Mountain gazelle, *Gazella gazella gazella*. *Israel Journal of Zoology* **23**, 39–44.

Baharav, D. (1983). Reproductive strategies in female Mountain and Dorcas gazelles (*Gazella gazella* and *Gazella dorcas*). *Journal of Zoology (London)* **200**, 445–453.

Bar-Matthews, M., Ayalon, A. & Kaufman, A. (1998). Palaeoclimate evolution in the eastern Mediterranean region during the last 58,000 years as derived from stable isotopes of speleothems (Soreq Cave, Israel). *Isotope Techniques in the Study of Environmental Change (Proceedings of an International Symposium on Isotope Techniques in the Study of Past and Current Environmental Changes in the Hydrosphere and the Atmosphere)*. IAEA-SM-349/17. Vienna: International Atomic Energy Agency, pp. 673–682.

Bar-Matthews, M., Ayalon, A., Kaufman, A. & Wasserburg, G. J. (1999). The eastern Mediterranean paleoclimate as a reflection of regional events: Soreq Cave, Israel. *Earth and Planetary Science Letters* **166**, 85–95.

Bar-Yosef, O. (1991). The history of excavations at Kebara Cave. In (O. Bar-Yosef & B. Vandermeersch, Eds.) *Le Squelette Moustérien de Kébara 2*. Cahiers de Paléoanthropologie. Paris: Editions du Centre National de la Recherche Scientifique, pp. 17–27.

Bar-Yosef, O., Vandermeersch, B., Arensburg, B., Belfer-Cohen, A., Goldberg, P., Laville, H., Meignen, L., Rak, Y., Speth, J. D., Tchernov, E., Tillier, A.-M. & Weiner, S. (1992). The excavations in Kebara Cave, Mt. Carmel. *Current Anthropology* **33**, 497–550.

Baryshnikov, G., Hoffecker, J. F. & Burgess, R. L. (1996). Paleontology and zooarchaeology of Mezmaiskaya Cave (northwestern Caucasus, Russia). *Journal of Archaeological Science* **23**, 313–335.

Binford, L. R. (1978). *Nunamiut Ethnoarchaeology*. New York: Academic Press.

Binford, L. R. (1981). *Bones: Ancient Men and Modern Myths*. New York: Academic Press.

Binford, L. R. (1984). *Faunal Remains from Klasies River Mouth*. Orlando, FL: Academic Press.

Binford, L. R. (1987). Were there elephant hunters at Torralba? In (M. H. Nitecki & D. V. Nitecki, Eds.) *The Evolution of Human Hunting*. New York: Plenum Press, pp. 47–106.

Binford, L. R. (1988). Etude taphonomique des restes fauniques de la Grotte Vaufrey. In (J.-P. Rigaud, Ed.) *La Grotte Vaufrey à Cénac et Saint-Julien (Dordogne): Paléoenvironnements, Chronologie et Activités Humaines*. Mémoire 19. Paris: Société Préhistorique Française, pp. 535–564.

Boëda, E., Geneste, J.-M., Griggo, C., Mercier, N., Muhesen, S., Reyss, J. L., Taha, A. & Valladas, H. (1999). A Levallois point embedded in the vertebra of a wild ass (*Equus africanus*): Hafting, projectiles and Mousterian hunting weapons. *Antiquity* **73**, 394–402.

Blasco, M. F., Montes, L. & Utrilla, P. (1996). Deux modèles de stratégie occupationelle dans le Moustérien tardif de la Vallée de l'Ebre: Les Grottes de Peña Miel et Gabasa. In (E. Carbonell & M. Vaquero, Eds.) *The Last Neandertals, the First Anatomically Modern Humans: A Tale About the Human Diversity. Cultural Change and Human Evolution: The Crisis at 40 KA BP*. Tarragona, Spain: Grafiques Lluc, pp. 289–313.

Boyle, K. V. (1998). *The Middle Palaeolithic Geography of Southern France: Resources and Site Location*. BAR International Series 723. Oxford: British Archaeological Reports.

Brooks, A. S. (1996). Open air sites in the Middle Stone Age of Africa. In (N. J. Conard & F. Wendorf, Eds.) *Workshop 5. Middle Palaeolithic and Middle Stone Age Settlement System*. International Union of Prehistoric and Protohistoric Sciences. The Proceedings of the XIII International Congress of Prehistoric and Protohistoric Sciences, Forli, Italy, 8–14 September 1996, Vol. 6. Workshops, Tome 1. Forli, Italy Forli, Italy: A.B.A.C.O. Edizioni, pp. 249–253.

Brugal, J.-P., Meignen, L. & Patou-Mathis, M. (Eds.) (1998). *Economie Préhistorique: Les Comportements de Subsistance au Paléolithique*. XVIII^{e} Rencontres Internationales d'Archéologie et d'Histoire d'Antibes. Sophia Antipolis, France: Editions APDCA (Association pour la Promotion et la Diffusion des Connaissances Archéologiques).

Bunn, H. T. (1991). A taphonomic perspective on the archaeology of human origins. *Annual Review of Anthropology* **20**, 433–467.

Burke, A. M. (2000). The view from Starosele: Faunal exploitation at a Middle Palaeolithic site in western Crimea. *International Journal of Osteoarchaeology* **10**, 325–335.

Chapman, D. I. & Chapman, N. G. (1975). *Fallow Deer: Their History, Distribution and Biology*. Lavenham, Suffolk, England: Terence Dalton.

Chase, P. G. (1986). *The Hunters of Combe Grenal: Approaches to Middle Paleolithic Subsistence in Europe*. BAR International Series 286. Oxford: British Archaeological Reports.

Chase, P. G. (1988). Scavenging and hunting in the Middle

Paleolithic: The evidence from Europe. In (H. L. Dibble & A. Montet-White, Eds.) *Upper Pleistocene Prehistory of Western Eurasia*. University Museum Monograph 54, University Museum Symposium Series 1. Philadelphia: University of Pennsylvania, The University Museum, pp. 225–232.

Conard, N. J. & Prindiville, T. J. (2000). Middle Palaeolithic hunting economies in the Rhineland. *International Journal of Osteoarchaeology* **10**, 286–309.

Davis, S. J. M. (1977). The ungulate remains from Kebara Cave. In (B. Arensburg & O. Bar-Yosef, Eds.) *Moshé Stekelis Memorial Volume*. Eretz-Israel: Archaeological, Historical and Geographical Studies. Jerusalem: The Israel Exploration Society, pp. 150–163.

Davis, S. J. M. (1980). Late Pleistocene-Holocene gazelles of northern Israel. *Israel Journal of Zoology* **29**, 135–140.

Davis, S. J. M. (1980). A note on the dental and skeletal ontogeny of *Gazella*. *Israel Journal of Zoology* **29**, 129–134.

Davis, S. J. M. (1983). The age profiles of gazelle predated by ancient man in Israel: Possible evidence for a shift from seasonality to sedentism in the Natufian. *Paléorient* **9**, 55–62.

Davis, S. J. M. (1987). *The Archaeology of Animals*. London: B. T. Batsford.

Davis, S. J. M., Lernau, O. & Pichon, J. (1994). The animal remains: New light on the origin of animal husbandry. In (M. Lechevallier & A. Ronen, Eds.) *Le Gisement de Hatoula en Judée Occidentale, Israël*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem 8. Paris: Association Paléorient, pp. 83–100.

Davis, S. J. M., Rabinovich, R. & Goren-Inbar, N. (1988). Quaternary extinctions and population increase in western Asia: The animal remains from Biq'at Quneitra. *Paléorient* **14**, 95–105.

Díez, J. C., Fernández-Jalvo, Y., Rosell, J. & Cáceres, I. (1999). Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). *Journal of Human Evolution* **37**, 623–652.

Dunham, K. M. (1997). Population growth of Mountain Gazelles *Gazella gazella* reintroduced to central Arabia. *Biological Conservation* **81**, 205–214.

Farizy, C., David, F. & Jaubert, J. (1994). *Hommes et Bisons du Paléolithique Moyen à Mauran (Haute-Garonne)*. Supplément à Gallia Préhistoire 30e. Paris: CNRS Editions.

Frankenberg, E. (1992). Management of Mountain Gazelle in Israel. In (F. Spitz, G. Janeau, G. Gonzalez & S. Aulagnier, Eds.) *Ongulés/Ungulates 91*. Paris and Toulouse: S.F.E.P.M.-I.R.G.M., pp. 353–355.

Gaudzinski, S. (1995). Wallertheim revisited: A re-analysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhessen/Germany). *Journal of Archaeological Science* **22**, 51–66.

Gaudzinski, S. (1996). On bovid assemblages and their consequences for the knowledge of subsistence patterns in the Middle Palaeolithic. *Proceedings of the Prehistoric Society* **62**, 19–39.

Gaudzinski, S. & Roebroeks, W. (2000). Adults only: Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, northern Germany. *Journal of Human Evolution* **38**, 497–521.

Gifford-Gonzalez, D. P. (1991). Examining and refining the quadratic crown height method of age estimation. In (M. C. Stiner, Ed.) *Human Predators and Prey Mortality*. Boulder, CO: Westview Press, pp. 41–78.

Grayson, D. K., Delpech, F., Rigaud, J.-P. & Simek, J. F. (2001). Explaining the development of dietary dominance by a single ungulate taxon at Grotte XVI, Dordogne, France. *Journal of Archaeological Science* **28**, 115–125.

Haltenorth, T. (1959). Beitrag zur Kenntnis des Mesopotamischen Damhirsches – *Cervus (Dama) mesopotamicus* Brooke, 1875 – und zur Stammes- und Verbreitungsgeschichte der Damhirsche Allgemein. *Säugetierkundliche Mitteilungen* **7**, 1–89.

Hayden, B. (1993). The cultural capacities of Neandertals: A review and re-evaluation. *Journal of Human Evolution* **24**, 113–146.

Hoffecker, J. F. & Cleghorn, N. (2000). Mousterian hunting patterns in the northwestern Caucasus and the ecology of the Neanderthals. *International Journal of Osteoarchaeology* **10**, 368–378.

Horwitz, L. K., Cope, C. & Tchernov, E. (1990). Sexing the bones of Mountain Gazelle (*Gazella gazella*) from prehistoric sites in the southern Levant. *Paléorient* **16**, 1–11.

Jaubert, J., Lorblanchet, M., Laville, H., Slott-Moller, R., Turq, A. & Brugal, J.-P. (1990). *Les Chasseurs d'Aurochs de la Borde: Un Site du Paléolithique Moyen (Livernon, Lot)*. Documents d'Archéologie Française 27. Paris: Editions de la Maison des Sciences de l'Homme.

Klein, R. G. (1987). Reconstructing how early people exploited animals: Problems and prospects. In (M. H. Nitecki & D. V. Nitecki, Eds.) *The Evolution of Human Hunting*. New York: Plenum Press, pp. 11–46.

Klein, R. G. (1989). Why does skeletal part representation differ between smaller and larger bovids at Klasies River Mouth and other archaeological sites? *Journal of Archaeological Science* **16**, 363–381.

Klein, R. G. (1999). *The Human Career: Human Biological and Cultural Origins*. 2nd ed. Chicago: University of Chicago Press.

Klein, R. G. (2003). Whither the Neanderthals? *Science* **299**, 1525–1527.

Klein, R. G. & Cruz-Uribe, K. (1984). *The Analysis of Animal Bones from Archaeological Sites*. Chicago: University of Chicago Press.

Lincoln, G. A. (1992). Biology of seasonal breeding in deer. In (R. D. Brown, Ed.) *The Biology of Deer: Proceedings of the International Symposium on the Biology of Deer, Mississippi State University, May 28–June 1, 1990*. New York: Springer-Verlag, pp. 565–574.

Loudon, A. S. I. & Brinklow, B. R. (1992). Reproduction in deer: Adaptations for life in seasonal environments. In (R. D. Brown, Ed.) *The Biology of Deer: Proceedings of the International Symposium on the Biology of Deer, Mississippi State University, May 28–June 1, 1990*. New York: Springer-Verlag, pp. 261–278.

Lyman, R. L. (1994). *Vertebrate Taphonomy*. Cambridge Manuals in Archaeology. Cambridge: Cambridge University Press.

Marean, C. W. & Kim, S. Y. (1998). Mousterian large-mammal remains from Kobeh Cave: Behavioral implications for Neanderthals and Early Modern Humans. *Current Anthropology* **39** (Supplement), S79–S113.

Mendelssohn, H. & Yom-Tov, Y. (1987). Chapter 7: Mammals. In (A. Alon, Ed.) *Plants and Animals of the Land of Israel*. Tel Aviv: Israel Defense Ministry Publishing House (in Hebrew).

Milo, R. G. (1998). Evidence for hominid predation at Klasies River Mouth, South Africa, and its implications for the behaviour of Early Modern Humans. *Journal of Archaeological Science* **25**, 99–133.

O'Connell, J. F., Hawkes, K. & Blurton Jones, N. G. (1988). Hadza hunting, butchering, and bone transport and their archaeological implications. *Journal of Anthropological Research* **44**, 113–162.

O'Connell, J. F., Hawkes, K. & Blurton Jones, N. G. (1990). Reanalysis of large mammal body part transport among the Hadza. *Journal of Archaeological Science* **17**, 301–316.

Patou-Mathis, M. (2000). Neanderthal subsistence behaviours in Europe. *International Journal of Osteoarchaeology* **10**, 379–395.

SAS Institute, Inc. (1998). *StatView Reference*. 2nd ed. Cary, NC: SAS Institute, Inc.

Schick, T. & Stekelis, M. (1977). Mousterian assemblages in Kebara Cave, Mount Carmel. In (B. Arensburg & O. Bar-Yosef, Eds.) *Moshé Stekelis Memorial Volume*. Eretz-Israel: Archaeological, Historical and Geographical Studies. Jerusalem: The Israel Exploration Society, pp. 97–149.

Sokal, R. R. & Rohlf, F. J. (1969). *Biometry: The Principles and Practice of Statistics in Biological Research*. San Francisco: W. H. Freeman.

Speth, J. D. (1983). *Bison Kills and Bone Counts: Decision Making by Ancient Hunters*. Chicago: University of Chicago Press.

Speth, J. D. & Tchernov, E. (1998). The role of hunting and scavenging in Neandertal procurement strategies: New evidence from Kebara Cave (Israel). In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds.) *Neandertals and Modern Humans in Western Asia*. New York: Plenum Press, pp. 223–239.

Speth, J. D. & Tchernov, E. (2001). Neandertal hunting and meat-processing in the Near East: Evidence from Kebara Cave (Israel). In (C. B. Stanford & H. T. Bunn, Eds.) *Meat-Eating and Human Evolution*. The Human Evolution Series. Oxford: Oxford University Press, pp. 52–72.

Speth, J. D. & Tchernov, E. (2002). Middle Paleolithic tortoise use at Kebara Cave (Israel). *Journal of Archaeological*

Science **29**, 471–483.

Spinage, C. A. (1971). Geratodontology and horn growth of the Impala (*Aepyceros melampus*). *Journal of Zoology (London)* **164**, 209–225.

Spinage, C. A. (1973). A review of the age determination of mammals by means of teeth, with especial reference to Africa. *East African Wildlife Journal* **11**, 165–187.

Spinage, C. A. (1976). Age determination of the female Grant's Gazelle. *East African Wildlife Journal* **14**, 121–134.

Stiner, M. C. (1994). *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton, NJ: Princeton University Press.

Stiner, M. C. (2002). Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* **10**, 1–63.

Stiner, M. C., Munro, N. D. & Surovell, T. A. (2000). The tortoise and the hare: Small-game use, the broad-spectrum revolution, and Paleolithic demography. *Current Anthropology* **41**, 39–73.

Stiner, M. C., Munro, N. D., Surovell, T. A., Tchernov, E. & Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal exploitation. *Science* **283**, 190–194.

Stiner, M. C. & Tchernov, E. (1998). Pleistocene species trends at Hayonim Cave: Changes in climate versus human behavior. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds.) *Neandertals and Modern Humans in Western Asia*. New York: Plenum Press, pp. 241–262.

Stringer, C. B. & McKie, R. (1997). *African Exodus: The Origins of Modern Humanity*. London: Pimlico.

Thieme, H. (1997). Lower Paleolithic hunting spears from Germany. *Nature* **385**, 807–810.

Tortosa, J. E. A., Villaverde Bonilla, V., Perez Ripoll, M., Martınez Valle, R. & Guillem Calatayud, P. (2002). Big game and small prey: Paleolithic and Epipaleolithic economy from Valencia (Spain). *Journal of Archaeological Method and Theory* **9**, 215–268.

Valensi, P. (2000). The archaeozoology of Lazaret Cave (Nice, France). *International Journal of Osteoarchaeology* **10**, 357–367.

Valladas, H., Joron, J.-L., Valladas, G., Arensburg, B., Bar-Yosef, O., Belfer-Cohen, A., Goldberg, P., Laville, H., Meignen, L., Rak, Y., Tchernov, E., Tillier, A.-M. & Vandermeersch, B. (1987). Thermoluminescence dates for the Neanderthal burial site at Kebara in Israel. *Nature* **330**, 159–160.

Villaverde, V., Martinez-Valle, R., Guillem, P. M. & Fumanal, M. P. (1996). Mobility and the role of small game in the Middle Paleolithic of the central region of the Spanish Mediterranean: A comparison of Cova Negra with other Paleolithic deposits. In (E. Carbonell & M. Vaquero, Eds.) *The Last Neandertals, the First Anatomically Modern Humans: A Tale About the Human Diversity. Cultural Change and Human Evolution: The Crisis at 40 KA BP*. Tarragona, Spain: Grafiques Lluc, pp. 267–288.

Chapter XII

Wetland Drainage in the Levant (Lake Hula, Amik Gölü, and el-Azraq Oasis): Impact on Avian Fauna

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Abstract

Human-induced drainage during the mid-twentieth century has caused the loss of the three large and rich wetlands of the Levant: Lake Hula (35°43′ E, 33°03′ N) in northern Israel (drained during 1950–1958), Amik Gölü (Lake Amik, Lake Antioch, or Bahr el-Abiad) in southeastern Turkey (drained during 1950–1975), and el-Azraq Oasis (36°48′ E, 31°49′ N) in the Hashemite Kingdom of Jordan (drained during 1950–1993). The consequences were loss of most of their avian populations, together with other invaluable indigenous fauna and flora groups. In terms of bird movements, Lake Hula, Amik Gölü, and el-Azraq Oasis are closely related. It is supposed that changes that occurred in each of the wetlands are reflected in the structure of the avian population in the others. While the interactions between Lake Hula and Amik Gölü were mainly of breeding and wintering bird populations, those between Lake Hula and el-Azraq Oasis probably consisted of migrating and wintering populations. This study aims to cast light on the possible inter-relationships among these former wetlands in order to understand the role of each of the habitats in the avian regional resource partitioning. There is some evidence that Amik Gölü's breeding populations of Darter, *Anhinga melanogaster chantrei*, wintered regularly in Lake Hula. The influx of Squacco Heron, *Ardeola ralloides* (1961), Black-crowned Night Heron, *Nycticorax nycticorax* (1963), Little Egret, *Egretta garzetta* (1967), and Glossy Ibis, *Plegadis falcinellus* (1975), into the breeding heron colony of Lake Hula is attributed to the gradual draining stages of Amik Gölü. Similarly, there was an increase in the wintering populations of European Coot, *Fulica atra*, and Teal, *Anas crecca*, with some other duck species, in Israel during the early 1970's. The influx of the Cattle Egret, *Bubulcus ibis* (1975), is attributed to the combination of certain changes in its habitat in Africa, its consequent spreading to Europe, and the drainage of Amik Gölü. The inter-relationships between el-Azraq Oasis and Lake Hula were through the eastern flyway of migrating avian populations, such as Shelduck, *Tadorna tadorna*, which probably use Lake Hula as an alternative habitat in years when the seasonal lake in the oasis (Qa el-Azraq) does not hold water. The available indirect evidence of the relationships among species and specific habitats may be of help in suggested regional rehabilitation programs of the Levant wetlands, particularly for species whose populations may be in jeopardy. Lake Hula and Amik Gölü should be designated for fish-eating and wintering avian populations by rehabilitation of deeper water bodies, Amik Gölü for large reedbeds and pebble-bed habitats for reed nesting and roosting species, and el-Azraq Oasis and Qa el-Azraq for eastern flyway migrating populations and several endangered desert species. To complete the variety of habitats, Sabkhat al-Jabbul in Syria should be preserved as a shallow saline lake as a food resource and nesting site for endangered species.

Introduction

Three large and important wetlands consisting of lakes, swamps, and seasonally inundated mudflats existed in the

Levant until the early 1950's: Lake Hula in northern Israel and, in the east, Amik Gölü (also known as Lake Amik, Lake Antioch, or Bahr el-Abiad, henceforth referred to here as Amik Gölü) in southeastern Turkey, and el-Azraq Oasis with its brackish lake in the Hashemite Kingdom of Jordan (Figure 1). Human-induced changes during the mid-twentieth century has caused the loss of these wetlands and, as a consequence, the loss of most of their avian populations together with other invaluable indigenous fauna and flora groups. All three wetlands harbored unique water-associated fauna and flora with large and diverse waterbird populations. Some of the species occurred in all three, probably with a certain amount of movement and interchange between sites. However, each area had its own unique species according to its geographic position, water quality, and specific habitats.

Lake Hula is ca. 170 km northwest of el-Azraq Oasis and ca. 370 km south of Amik Gölü (Figure 1). In terms of bird movements, all three are closely related. It is supposed that changes that occurred in each of the wetlands are reflected in the structure of the avian populations in the others. While the interactions between Lake Hula and Amik Gölü are probably mainly of breeding and wintering bird populations, the relations between el-Azraq Oasis and Lake Hula seem to consist of migrating and wintering populations. Migration across deserts usually proceeds over a broad front; therefore, el-Azraq Oasis and the Jordan Rift Valley (ca. 100 km to the west, with Lake Hula at its northern edge) are virtually one area as far as birds are concerned. This assumption was supported by Andrews (1996), who noted the east-west flyway of raptors between el-Azraq Oasis and Amman up to the eastern edge of the Rift Valley.

Distribution of avian fauna in wetlands depends mainly on available habitats, and the diversity of the population is a function of the diversity of the habitats. During recent decades, much biological diversity has been irreversibly lost through extinction caused by the accelerated destruction of natural habitats. Historically, the greatest threat to wetlands has been drainage and, in the last few decades, reduction of water input, especially from ground water. Changing land use by drainage of wetlands and turning it into agricultural land has played a leading role in the destruction and deterioration of wetlands in all parts of the Mediterranean region, as well as in other parts of the world (Garcia-Orcoyen Tormo et al. 1992).

Avian fauna are well known for their mobility and ability to use different sites for different functions. Their movements between wintering and summering (breeding) sites are well documented in recent ornithological literature. Despite the lack of modern technology for tracing movements of birds before the drainage of the Levant wetlands, there is some evidence that at least a few species alternated between the large wetlands in different seasons. Unfortunately, there is no direct evidence for determining the inter-relationships among the wetlands. However, the collated data from these former large wetlands of the Levant, and in particular from the draining process, indicate that operations extended over almost four decades. This information supports indirect evidence for explaining possible changes and movements in the avian populations as a response to habitat change in different draining stages.

This study aims to cast light on the possible inter-relationships among the three historically most important wetlands of the Levant (Lake Hula, Amik Gölü, and el-Azraq Oasis) in order to understand the role of each of them in avian regional resource partitioning. In addition, case studies of the draining process of the largest lakes of the Levant during a relatively short period give some insight into the use of habitats by the avifauna. Available indirect evidence of the relations between species and specific habitats may be of help in future management programs, in particular for species whose populations may be in jeopardy. In regions where water resources are limited, like the Levant, such regional programs have great value in the conservation of typical fauna and flora, especially endemic species which otherwise are condemned to extinction.

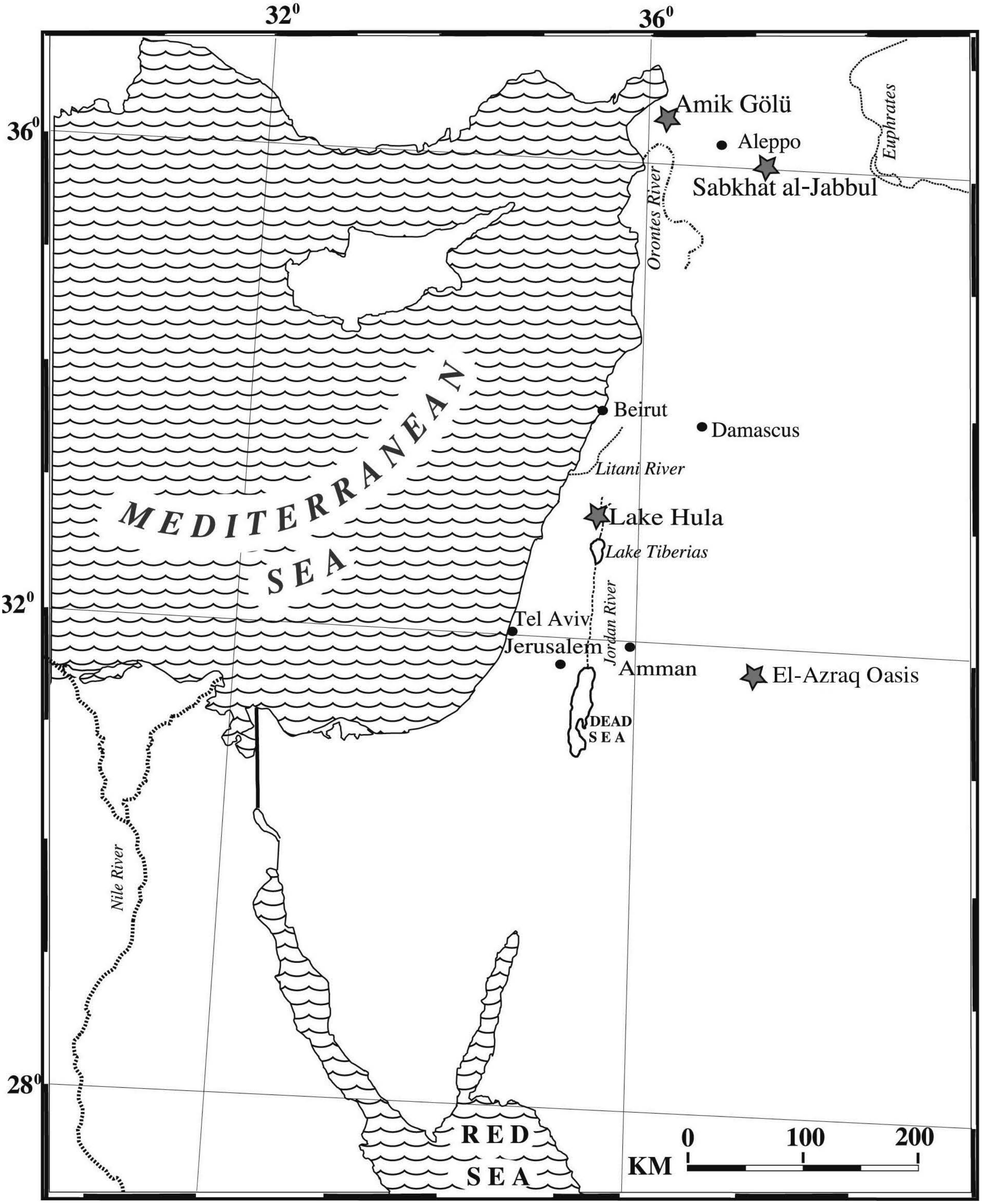
32⁰
36⁰
36⁰
32⁰
28⁰
Amik Gölü
Aleppo
Sabkhat al-Jabbul
Euphrates
Orontes River
MEDITERRANEAN SEA
Beirut
Damascus
Litani River
Lake Hula
Lake Tiberias
Jordan River
Tel Aviv
Jerusalem
Amman
El-Azraq Oasis
DEAD SEA
Nile River
RED SEA
0 100 200
KM

Figure 1. Regional map of the former large wetlands of the Levant. Stars denote the main wetlands mentioned in the text (base map drawn by Eitan Tchernov).

The former large lakes of the Levant

The draining of the lakes of the Levant started in the 1950's. Lake Hula was drained during 1950–1958, Amik Gölü during 1950–1975, and el-Azraq Oasis during 1950–1993 (Table 1). Lake Hula is the best documented among the three, as shown in the comprehensive and updated data collation provided by Dimentman et al. (1992), relating to the fauna and flora of the region both before and after drainage. For el-Azraq Oasis, Nelson (1973) provides comprehensive, though little updated, information on the avifauna and scattered information on other aspects of the fauna and flora before drainage. Other publications deal with the molluscs (Burch 1985) and avian fauna before and during drainage (Hollom 1959; Cameron & Cornwallis 1966; Mountfort 1966; Clarke 1980; Conder 1981; Wallace 1982, 1983, 1984), while Evans (1994) and Andrews (1995, 1996) compare the avian fauna of before and after drainage. Amik Gölü is the least known of the three lakes, as the available information on the lake was documented in publications that appeared in several languages (German, French, Turkish, English) and do not have a broad distribution. Information on the molluscs (Locard 1883; Schütt 1993), fish (Gruvel 1931), and avifauna (Tristram 1882; Aharoni 1930, 1943) was published long before drainage started. Later studies from the draining period are mainly on the avifauna or specific bird species of the lake (Hollom 1959; Kumerloeve 1960, 1963, 1964, 1966, 1969, 1970, 1984, 1989; Acar 1972; Karaca 1987; Akçakaya 1989; Kasparek et al. 1989; Kasparek 1992). Locard (1883) emphasizes the similarity in aquatic mollusc fauna of Amik Gölü and Lakes Tiberias (Kinneret) and Homs despite the distances between them and their different water compositions. Among the three, Locard refers to Amik Gölü as the most diverse in mollusc species. It has been shown that, while Lake Hula and Amik Gölü have many species of fish in common, each of them also has its own particular fauna (Gruvel 1931).

The main interest of this study is the water-associated birds of the lakes. An avian species list with information on the breeding species in each of the wetlands is given in the Appendix.

Lake Hula

Before drainage, Lake Hula and its swamps (35°43′ E, 33°03′ N) fluctuated annually between 21 km^2 in summer and 60 km^2 during winter floods. The open lake area was about 12–14 km^2, with a maximum depth of 3–4 m and an elevation of 70 m above sea level (Dimentman et al. 1992). The lake was fed by the Jordan River, whose headwaters are near Mount Hermon and the Dan springs. The outlet of the lake was the continuation of the Jordan River, which flowed into Lake Kinneret. Most of the swamps north of the lake were covered by stands of *Cyperus papyrus* (130–190 ha) with some open surface ponds (Zohary & Orshanski 1947; Dimentman et al. 1992). Lake Hula is considered the last limnic spot facing the Saharo-Arabian desert belt. The aquatic fauna of the Hula Valley present the highest reported diversity of aquatic fauna in the Levant (Por & Dimentman 1989; Dimentman et al. 1992). Although the diverse groups of aquatic fauna of Lake Hula are well documented, studies on its avian fauna before drainage are scarce compared to the other two wetlands. Apart from the study on the breeding species carried out during the draining process (Zahavi 1957), no avian population studies or regular counts of wintering populations have been conducted. For further information on the lake, the reader is referred to Dimentman et al. (1992), which provides data on a large series of faunal and floral taxa, accompanied by a series of maps on the distribution of vegetation belts and specific species of aquatic fauna, and a comprehensive list of over 500 publications on the lake.

The draining of Lake Hula started in 1951 and ended in 1958 (Table 1). After drainage a small portion (ca. 7%) was reconstructed and flooded in two stages. First, the Hula Nature Reserve in the northwest part of the former lake (3.2 km^2) was created in 1958 during the last stage of drainage (Dimentman et al. 1992). Thirty-six years later, in 1994, another part of the former Lake Hula was dug and flooded. The newly created Lake Agmon (1 km^2) is located about 2 km northeast of the Hula Nature Reserve (Hambright & Zohary 1998). The two sites are

Table 1. Stages in the draining process of the large wetlands of the Levant.

Date	Main Changes	Source
	Lake Hula	
Until 1950	The lake 5.3 x 4.4 km, extending 12-14 km^2	Dimentman et al. 1992
	The lake and swamps covered up to 60 km^2	Dimentman et al. 1992
1951	Drainage started	Karmon 1953, 1960
1958	3.5 km^2 inundated for conservation	Dimentman et al. 1992
1959	Loss of water by seepage and collapse of embankments	Dimentman et al. 1992
1964	The area declared as the first nature reserve in Israel	Dimentman et al. 1992
1968	Fishing and tourist boating ceased	Dimentman et al. 1992
1971	Intensive works to prevent water seepage	Dimentman et al. 1992
1972	Final works of rehabilitation of the Nature Reserve	Dimentman et al. 1992
1958–1993	Underground peat fires, soil subsidence, and inundation	
	Loss of endemic and unique species	
1994	Creation of Lake Agmon 1 km^2, 35°43′ E, 33°03′ N	Hambright & Zohary 1998
2002	7% of the former Lake Hula rehabilitated	
	Amik Gölü	
Early 1900's	Lake and swamps covered 350 km^2	Kumerloeve 1963
Before 1950	Lake and surroundings reduced to 310 km^2	Kumerloeve 1989
1950's	Drainage started, lake reduced to 280 km^2	Akçakaya 1989
1953	Lake still large, accessible by small boats	Kumerloeve 1989
1956	Draining operations in progress	Hollom 1959
	Sites previously holding Ardeids, amphibia, turtles - dried	Kumerloeve 1963
	Marshes converted to cotton fields; lake reduced to 90 km^2	Kumerloeve 1963
	Grazing by cattle and horses instead of water buffalo	Kumerloeve 1989
1960's	Main drainage operations	Kumerloeve 1963
	Waterbirds moved to drainage ditches	Kumerloeve 1989
1962	Lake surface water 60 km^2, water depth up to 70–80 cm	Kumerloeve 1963
	Fishing impossible, continued only in Lake Göl Basi	
1967	Only 46 km^2 of the lake remained	Varisligil 1968
1970's	Drainage in final stages	Bahtiyar Kurt
1975	Lake drained	Kumerloeve 1989
Late 1980's	Marshes recreated by inundation	Kasparek et al. 1989
1995	250 ha marsh remained near Göl Basi	Magnin & Yarar 1997
2002	Seasonal inundation and small lake in Göl Basi	Bahtiyar Kurt (pers. comm.)
	El-Azraq Oasis	
1950's	Pumping from Ein Qasiyah spring (water supply to Irbid)	Conder 1981
After 1974	Main source of swamp water, Wadi Rajil, dammed in Syria	Conder 1981
1977	El-Azraq included in the international Ramsar convention	Conder 1981
1978	El-Azraq declared as a nature reserve by RSCN	Conder 1981
1979	Water retreated 800 m from Roman wall	Conder 1981
	Overgrazing by camels, water buffaloes, cows, and horses	
	Dramatic decrease in waterfowl, mainly in teal and mallard	
1980	About 5 km^2 of perennial water bodies remained	Krupp & Schneider 1989
	Five fish ponds dug	Andrews 1995
1980's	Pumping to supply water to city of Zarqa	Conder 1981
1985	Central marsh shrinking, reeds dying	Nelson 1985
1989	Spring ceased to flow, vegetation died out	Andrews 1995
1992	North springs dried up completely	Papayannis 1992
1993	Watertable dropped 12 m below ground, area mostly dried	
	Wadi Rajil dammed in Jordan, north of el-Azraq	Evans 1994
1994	Program for pumping part of the water back into el-Azraq	Evans 1994
1995	For the first time since 1988 the Qa and marsh inundated	Khoury 1996

closely related and together constitute the recent large wetlands of the Hula Valley.

Lake Hula is one of the oldest documented lakes in history, mentioned in the Tell el-Amarna letters of Pharaoh Amenhothep IV in the 14th century BC (Smith 1973). The lake and its shores played an important role in the anthropogenic life of prehistoric periods, as shown by the Pleistocene site (0.78 Ma) of Gesher Benot Ya'aqov (GBY) at the southern end of the former lake (Goren-Inbar et al. 2000) and the Natufian site of Eynan or Mallaha (0.013 Ma) on its western shore (Valla 1995). Eynan was the most important coastal spring, creating a short stenothermic stream running into Lake Hula (Dimentman et al. 1992).

Amik Gölü

The available information on Amik Gölü (Lake Antioch, Bahr el-Abiad) is summarized here in detail, since collated information on the lake is lacking, to provide a better understanding of the lake's environment and habitats.

Before its drainage, Amik Gölü (36°18′ E, 36°23′ N) was the largest freshwater lake in the Levant, occupying an area of about 350 km^2, including 22 km^2 of swamps and a maximum water depth of 4 m (Kumerloeve 1963). The lake was located in the Amik Valley at an elevation of 80 m below sea level (Gruvel 1931). The slow water flow along ca. 40 km with a slope of only 1 m created a large inundated area in the valley (Gruvel 1931). The lake was surrounded by an extensive marsh fed by two important rivers, the Afrin and the Kara Su (representing the northernmost section of the Rift Valley). The outflow of the lake was the Küçük Asi River, which runs about 15 km before it flows into the Orontes (Gruvel 1931; Por & Dimentman 1989). The Arabic name for Amik Gölü, Bahr el-Abiad, means "the White Sea" and probably derived from the milky color of the lake during melting of the snow in spring, while in summer the lake was blue and transparent (Locart 1883).

The lake was unique among lakes in the Levant in having a connection to the sea through the Orontes that enabled migration of elements from the sea into the lake. The northern part of the lake was covered with extensive marsh. Farther north the wetland consisted of another small lake, Göl Basi, with its former river Murat Pasa that flowed into those swamps (Kumerloeve 1963). The entire Amik Valley with its lake was under the French Mandate and belonged to Syria until 1939, when it became part of Turkey (Kumerloeve 1963). Amik Gölü harbored very diverse habitats, such as swamps with emergent vegetation, open surface water bodies, wet grasslands, and gravel-covered flats (Kumerloeve 1963). It was mentioned as early as 1555 as an excellent place for waterbirds (Belon 1555) and described as the most outstanding paradise for birds in the Near East (Kumerloeve 1963). Reeds (*Juncus* and *Phragmites*), which created barriers to canoes, covered the marshes mainly in the eastern half of the lake, and were used as a nesting habitat by large waterbirds (Hollom 1959). The area between the lake and the swamps included stands of *Tamarix* (Meinertzhagen 1935; Kumerloeve 1963). The northern swamps were covered with emergent vegetation, mainly stands of *Arundo donax*, and in the shallow parts there were large stands of *Nuphar* sp., *Nymphaea* sp., and *Ranunculus aquaticus* (Kumerloeve 1963). Among submerged plants, Kumerloeve (1963) mentions *Ceratophyllum*. The marshes contained a rich ensemble of animals such as wild pig, jackal, fox, otter, many species of aquatic birds, a large quantity of fish and frogs, freshwater turtles, water snakes, several mollusc species, and in particular rich and dense beds of Zebra-mussel, *Dreissena polymorpha*, embedded with *Corbicula*, very large specimens of *Anodonta*, and several *Unio* species (Gruvel 1931). Water buffalo grazed in the marshes before they were drained (Kumerloeve 1989).

The lake was one of the most important sources of fish. The most abundant fish in the lake was the Eel, *Anguilla*, of which 10,000–50,000 fish could be caught in a single day (Gruvel 1931). A dam for facilitating fishing and preventing the return of *Anguilla* to the sea already existed in 1930 along the southern part of the lake on the Kara Su River. Lortet (1883) describes large specimens of eel from Amik Gölü that were ca. 1.5 m long. Among the fish in the lake were some species with very limited distribution such as *Barbus chantrei* (Krupp 1985a).

Amik Gölü was very rich in its avifauna and harbored 190 species, of which about 70% were resident and wintering species (Koning 1973). The most important breeding species were darter, Great White Pelican, *Pelecanus onocrotalus*, and Purple Gallinule, *Porphyrio porphyrio* (Grimmett & Jones 1989). In addition, Glossy Ibis, *Plegadis falcinellus*, Mallard, *Anas platyrhynchos*, and Tufted Duck, *Aythya fuligula*, were among the regularly breeding avian species in Amik Gölü (Acar 1972). During winter the lake was the most important wintering ground for Teal, *Anas crecca,* and the most abundant waterbird was the European Coot, *Fulica atra* (Kumerloeve 1970). For a complete list of the birds of Amik Gölü, see the Appendix.

The reasons for draining Amik Gölü were very similar to the justifications given for draining Lake Hula. Plans for draining the Amik wetlands were already made in the 1930's, mainly because of the *Anopheles* mosquito that served as carriers of malaria, especially in the annually inundated Amik Valley (Gruvel 1931). However, in the late stages before drainage, the main reason for draining was probably the aim of gaining agricultural land, which was never achieved due to unexpected land management problems (Karaca 1987).

Draining started in the 1950's (Akçakaya 1989), continued through the 1960's, and was completed in the 1970's (Kumerloeve 1989). For further details of the draining process, see Table 1. In winter 1964/1965 the site still harbored extremely large numbers of birds: European Wigeon, *Anas penelope* (15,000–20,000), Pintail, *Anas acuta* (10,000–15,000), Northern Shoveler, *Anas clypeata* (8,000–10,000), Pochard, *Aythya ferina* (10,000), Tufted Duck (8,000), and several groups of White-headed Duck, *Oxyura leucocephala*, which probably bred in the lake (Kumerloeve 1970).

In 1967, only 46 km^2 of the lake remained (Varisligil 1968), but in wintering bird counts there were still about 162,000 waterbirds on the lake (Magnin & Yarar 1997). Today, there is a small lake, Göl Basi, with 250 ha of marsh and seasonally inundated land in the Amik Valley (Magnin & Yarar 1997; Bahtiyar Kurt, personal communication).

El-Azraq Oasis

El-Azraq Oasis (36°48′ E, 31°49′ N; ca. 73 km^2) has a special ecological significance, as it is located at the center of a large desert basin. In the north and west it consists of limestone hammada desert, in the south and east, basalt desert, and in the basin there were perennial springs and marshlands. Before drainage, the marsh was about 25 km^2 with at least 6–7 km^2 of permanent marsh and stands of Cattail, *Typha angustata*, up to 3.8 km^2 with a further 0.8 km^2 in association with Bulrush, *Scirpus* (Nelson 1973). The el-Azraq pools run out into open, meandering creeks, which feed the permanent marsh. Hollom (1959) described a large, bare brackish lake that may dry up in summer, small reed-grown fresh-water ponds, and meadow-like marsh. The seasonal playa lake of Qa el-Azraq to the southeast, with its scattered islands, muddy margin, and artesian pools with variable areas of standing water, is among the most important areas for migrating and wintering birds in the Middle East (Evans 1994). The marshland and its surroundings were covered with dense stands of cattail, bulrush, *Carex*, *Juncus*, *Arundo*, *Nitraria*, and *Tamarix* (Evans 1994).

The annual rainfall in the oasis is below 100 mm but floods seasonally create a lake as a part of a network of waters with a great variety of chemical compositions (Scates 1968). In 1989 the seasonal lake attained an area of 50 km^2 and held water to a depth of 2 m (Garrard et al. 1989). The salinity (sodium Na^+) of the el-Azraq water bodies ranges from 75 ppm in spring pools to 6,400 ppm in the temporarily inundated Qa el-Azraq (Scates 1968). The water bodies contained several fish species (Nelson 1973), but the only native fish in the oasis is the Cyprinid, *Aphanius sirhani* (Krupp & Schneider 1989). A few aquatic invertebrates were noted in The General Corporation for the Environment Protection (1998). The list of freshwater molluscs found in el-Azraq's various habitats includes: *Theodoxus jordani*, *T. michonii*, *Bithynia phialensis*, *Heleobia* spp., *Pseudamnicola* spp., *Melanoides* *tuberculatus*, *Melanopsis buccinoidea*, *M. costata*, *Radix natalensis*, and *Planorbis planorbis* (Burch 1985; nomenclature according to H. Mienis, personal communication). *Radix natalensis* has been found to be infected with several types of larval trematodes that are suspected to infect local fish, amphibians, reptiles, birds, and mammals (Burch 1985). About 50–100 feral water buffalo were grazing in the marshland in 1989 (Garrard et al. 1989). About 280 avian species from 41 different families were recorded, with at least 70 breeding or probably breeding species (Nelson 1973; Wallace 1983). The area is one of the most important wetlands for migrating species, including 25 raptors that are probably regular migrants at the site (Zalles & Bildstein 2000). In winter 1967 el-Azraq Oasis still harbored ca. 350,000 waterbirds, with large populations of teal (180,000), pintail (100,000), European coot (40,000), European wigeon (20,000) and tufted duck (5,000) (Nelson 1973). However, waterbird numbers in the site have recently declined, and even in rainy years such as winter 1991/1992 only 20,000 used the site (Evans 1994).

El-Azraq Oasis was designated in 1965 as a protected area, and in 1977 as a National Park (The General Corporation for the Environment Protection 1998) and as an important wetland under the Ramsar Convention (Nelson 1973; Conder 1981; Papayannis 1992). The draining process of the oasis was gradual and continuous from 1974 until the dramatic drop of the aquifer water table in 1993 (Table 1). In 1994 a new program started for rehabilitation of parts of the oasis by pumping a certain amount of groundwater back into the reserve. This program proved very successful, at least in 1995, when for the first time since 1988 the outer limits of the marsh (in addition to Qa el-Azraq) were inundated by spring water (Khoury 1996). There is no published information on the present situation of the oasis.

The drainage stages and their consequences

An attempt has been made to reconstruct the stages of the drainage process in each of the studied wetlands in order to detect possible effects on changes of populations. The historical events of the draining process in the large wetlands of the Levant, collated from various sources, are presented in Table 1.

Before drainage, Lake Hula harbored about 106 species of birds of which at least 40 were breeding species, 18 fish species, 24 gastropod species, six taxa of bivalves, 24 species of Ostracoda, 38 species of Cladocera, 21 species of Oligochaeta, 11 taxa of Hirudinea and many more groups. After drainage, 119 animal taxa were lost from the region, 37 of which were no longer recorded in Israel (Dimentman et al. 1992).

The drainage of Amik Gölü started in the 1950's and was completed by 1975 (Bahtiyar Kurt, personal communication; see Table 1). The Water Vole, *Arvicola terrestris*, a rodent that lived in both Amik Gölü and Lake Hula (Harrison & Bates 1991), disappeared from both sites after the drainage. At least ten endemic fish species became extinct as a consequence of the drainage. The most important of these are *Acanthobrama centisquama*, *Alburnus coeruleus*, *Barbus canis*, *Barbus orontis*, *Hemigrammocapoeta sauvagei*, *Pararhodeus kervillei*, *Phoxinellus zeregi*, *Tylognathus caudomaculatus*, *Capoeta barroisi*, and *Noemacheilus argyrogramma* (Kence 1987). Another was the mollusc-eating fish *Barbus lorteti* (Krupp 1985b; Kuru 1987). The unique endemic mollusc fauna described by Locard (1883) was probably lost. In the remaining part of the former lake, Göl Basi, beds of the bivalve *Dreissena caputlacus* still exist (Schütt 1993). The Darter, *Anhinga melanogaster chantrei*, an endemic avian subspecies, was first described in Turkey from Amik Gölü in 1882, as *Anhinga rufa chantrei* (Kumerloeve 1984). This form was confined to Amik Gölü and to the region of the Euphrates and Tigris Rivers. In the western Palearctic it exists only in southern Iraq (Akçakaya 1989). According to Tchernov (1980), these populations were probably cut off from the African populations during the late Neogene. This subspecies is now considered extinct in the Middle East. In addition, the drainage caused the loss of breeding populations of two pelican species, the great white pelican and the Dalmatian Pelican, *Pelecanus crispus*, and of the largest breeding population of the endangered purple gallinule subspecies, *Porphyrio porphyrio seistanicus* (Kumerloeve 1966). The white pelican breeding population consisted of about 2,500 breeding pairs (Kence 1987). The Amik Gölü populations of purple gallinule had whitish heads, a feature absent in other populations of the species (Kasparek et al. 1989).

El-Azraq Oasis underwent a continuous process of degradation from the late 1960's (Nelson 1973) until it almost totally dried up in the late 1980's (Andrews 1995). At least 20 bird species, including Little Grebe, *Tachybaptus ruficollis*, Little Bittern, *Ixobrychus minutus*, Squacco Heron, *Ardeola ralloides*, Purple Heron, *Ardea purpurea*, mallard, and Garganey, *Anas querquedula*, were lost as breeding species by 1993 (Andrews 1995). The number of migrating raptors declined to 182 in spring 1992 (Andrews 1996).

Despite some efforts to reconstruct parts of the former wetlands of the Levant, some of their unique floral and faunal elements have probably been lost. As mentioned above, Lake Hula, Amik Gölü, and el-Azraq Oasis were the three largest wetlands in the Levant, harboring almost the entire aquatic biodiversity of the Levant. The human-induced loss of these habitats, with their assemblage of species, has likely led to the destruction of the entire unique aquatic fauna of a region. The drainage left the Levant without alternatives for those species that survived and need specific habitats. The direct effect of the drainage on the avian fauna was not only on species that disappeared from the area, but also on changes in the breeding status of several species that lost their breeding habitats and were recorded later only as wintering.

Complementary utilization of Levant wetlands by avian populations

While the relations between Lake Hula and Amik Gölü seem to be characterized by the combined use by avian populations needing different habitats for breeding and wintering, the relations between Lake Hula and el-Azraq Oasis seem to be those of providing alternative habitats mainly for migratory populations.

Lake Hula as wintering site for Amik Gölü breeding populations

The darter used to breed in Amik Gölü and was a common winter visitor in Lake Hula (Aharoni 1943; Hardy 1946; Hovel 1987; Kasparek 1992). At least one hundred darters used to breed in the lake before its drainage (Kence 1987). In 1946 the species was very common during the winter in the Yarmuk estuary (Transjordan), but in about 1955 it became extinct in this region (Andrew 1995). According to Hovel (1987), up to 50 birds regularly visited Lake Hula in winter until 1955. Amik Gölü was suitable for the breeding of the darter, since before its complete drainage the lake contained fish species like *Mugil* and *Anguilla* that migrated from the open sea into the lake (Lortet 1883; Gruvel 1931; Por & Dimentman 1989). Aharoni (1943) described large shoals of eel as being the main fish food of the darter chicks that hatched in the breeding colony in the lake. In Lake Hula, darters fed mainly on cyprinoids but not on the spiny tilapia, since they might damage the bird's ingestive system (Aharoni 1943). Commercial fishponds that developed in the Hula Valley from 1940 (before the drainage of Lake Hula) caused a dramatic increase in the populations of the water snake, *Natrix tessellata* (Yom-Tov & Mendelssohn 1988). It is possible that this abundant species was a food resource for darters in Lake Hula during the winter.

The Hula Nature Reserve as refuge for Amik Gölü avian populations

Drainage operations first affect shallow parts and only in advanced stages the deeper parts of the lake. Consequently, colonial breeding species that nest in habitats with large stands of emergent reeds, such as herons, ibis, spoonbill, and cormorants, will be the first to react to drying wetland. Smaller species that are solitary breeders among reeds, such as European coot, moorhen, some ducks and warblers, will demonstrate some flexibility and greater resistance in the first draining stages as long as the emergent vegetation belts advance with the water line. The last species that will be affected are all the ducks that feed in open water but need a certain water level, such as pochard, tufted duck, teal, and northern shoveler.

Influx of wintering avian populations to the north of Israel

As shown for several breeding species, the unexplained increase in populations of several waterbirds (mainly wintering ducks) is thought to be the result of the final drainage of Amik Gölü during the early to mid-1970's. Figure 2 shows the increase in numbers of wintering European coot and teal (which were the most abundant wintering species at Amik Gölü) and all the anatids in northern Israel during the 1970's. As most of the wintering waterbirds were concentrated in the north and the coastal plain, and particularly in the Hula Valley, the data for the total area were used. The increase in the number of selected wintering species in northern Israel during the 1970's is attributed to the draining of Amik Gölü. Additional evidence of the relations between the populations of Lake Hula and Amik Gölü come from two specimens of teal that were ringed in Israel in the winters of 1969 and 1970 and were recorded in Turkey in 1971, one in winter and the other during the summer breeding season (Israel Bird Ringing Center unpublished data). As mentioned above, this species is a very common winter visitor to Israel and a wintering and breeding species in Amik Gölü (Koning 1973). It seems that populations of teal

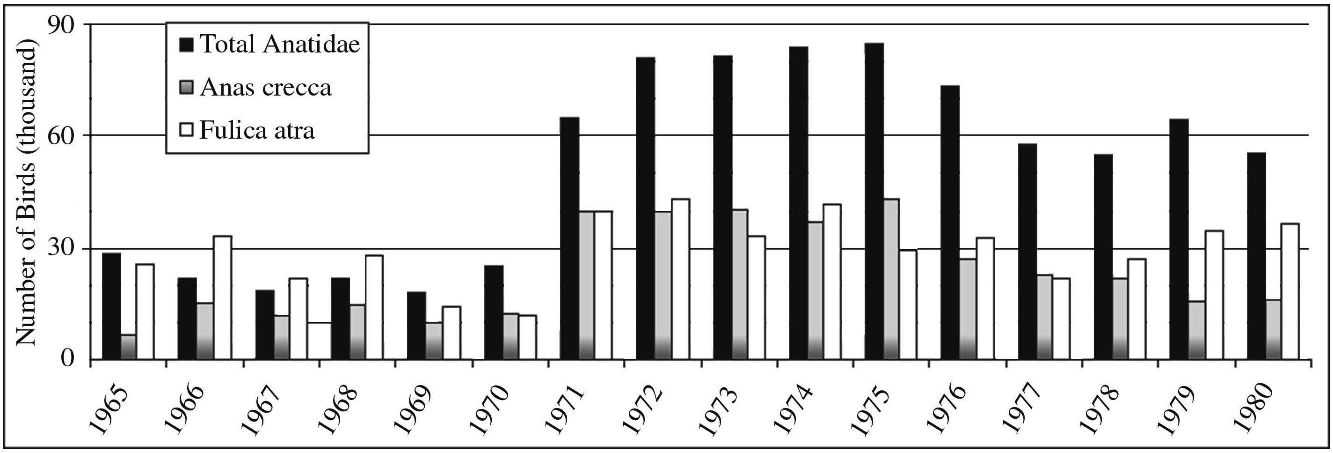

Figure 2. Trends in winter counts of selected waterbird populations in Israel. Based on Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980. Teal and European coot were the most abundant wintering species in Amik Gölü (see text).

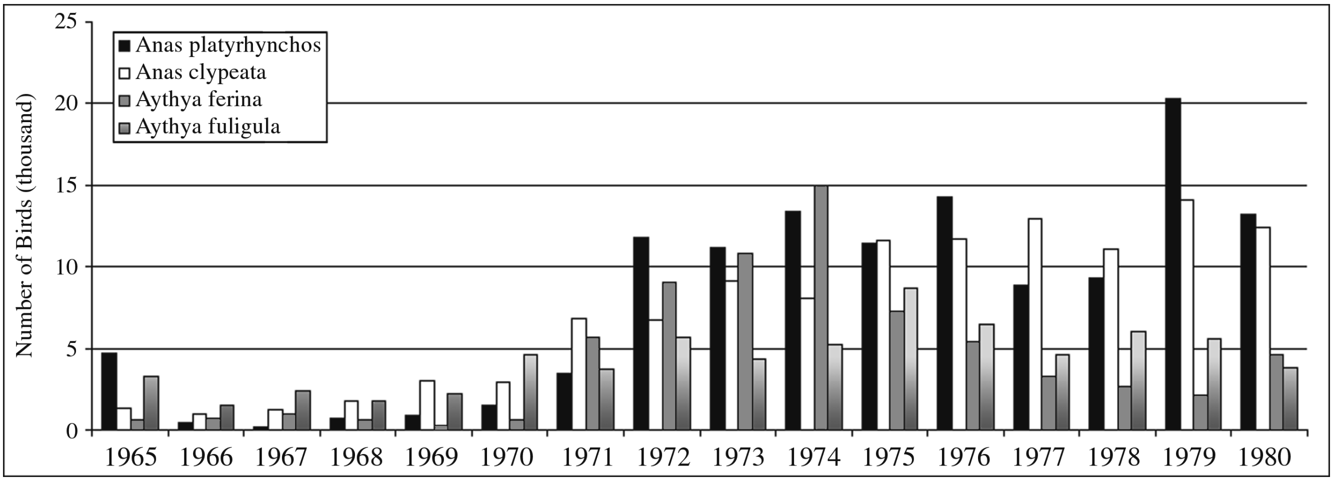

Figure 3. Trends in wintering populations of selected waterbirds in Israel. Based on Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980. The selected species were abundant in Amik Gölü (see text).

alternated between both lakes in winter but bred only in Amik Gölü.

The same trend of species that were abundant in winter in Amik Gölü but whose populations increased in Israel during the 1970’s is shown in Figure 3. Two of these species, mallard and tufted duck, were also breeding species in Amik Gölü. In this case as well, the increase in populations of wintering ducks in Israel during the 1970’s is attributed to the draining of Amik Gölü.

The increase in wintering populations cannot be attributed to increase in habitat, since during the early 1970’s there was no increase in available habitats for waterbirds such as commercial fishponds. The main changes in the water surface area of such ponds occurred before 1962 and did not change until 1979 (Ashkenazi & Yom-Tov 1997).

Changes in the Hula Nature Reserve breeding colony

There is some evidence that avian populations of Amik Gölü followed the scenario of gradual loss of habitats as the draining operations proceeded. Figure 4 shows the year in which different species joined the Lake Hula breeding colony. The purple heron and the little bittern have been the most stable breeding species in Lake Hula from 1948 and probably did not take part in the assumed influx of species from the drained Amik Gölü. The Grey Heron, *Ardea cinerea*, was one of the breeding populations of Lake Hula before drainage, although it ceased breeding in1964. Interestingly, this species also ceased breeding in Amik Gölü, probably in 1962 (Kumerloeve 1963). The squacco heron and the Black-crowned Night Heron, *Nycticorax nycticorax*, started breeding in the Lake Hula colony in 1961 and 1963, respectively. It seems that both species joined Lake Hula as a result of the proceeding drainage of Amik Gölü, as Kumerloeve (1963) mentions their declining populations in Amik Gölü in 1962. In the same year, Little Egret, *Egretta garzetta* were still abundant in Amik Gölü (Kumerloeve 1963), and this species joined the breeding colony at Lake Hula only later, in 1967. The breeding population in Israel increased from 50 pairs in 1971 to 550 pairs in 1973, and the wintering population increased in the same period by 300% (Suaretz & Paz 1975). This otherwise unexplained increase is attributed to the last draining stages of Amik Gölü.

The last species to join during the Amik Gölü drainage process were the Cattle Egret, *Bubulcus ibis*, and glossy ibis, in 1975. These breed in both mixed heron colonies and monospecies colonies, not necessarily near water. Among herons, the cattle egret is the least dependant on water in

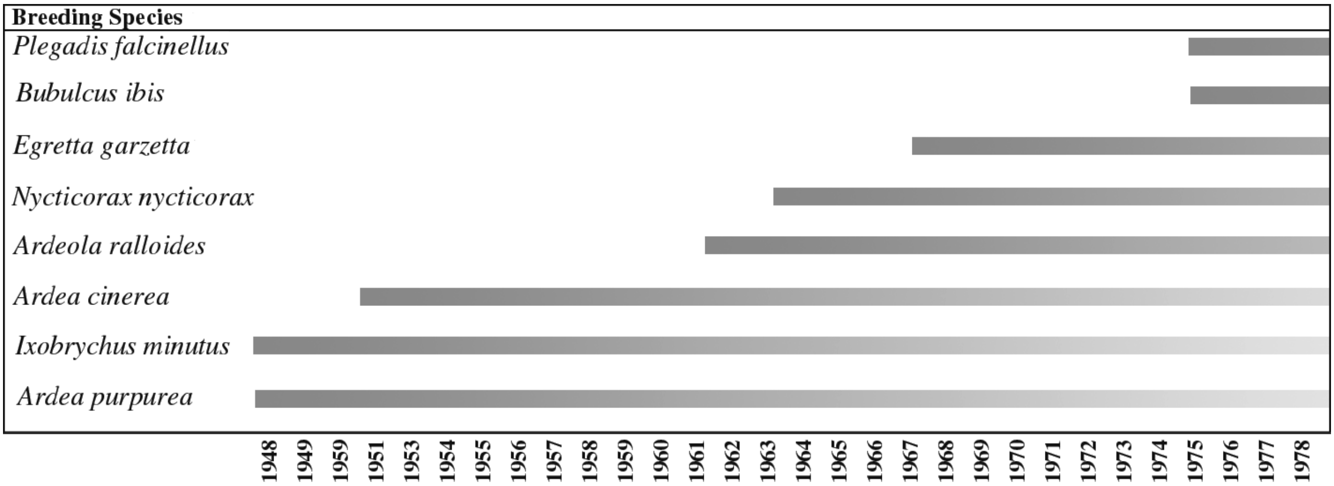

Figure 4. Changes in species composition of the Hula Nature Reserve breeding colony. Based on Suaretz & Paz (1975) and Ashkenazi & Yom-Tov (1997). From 1975 there were no changes until 1995, when *Phalacrocorax pygmeus* joined the colony (Ashkenazi & Yom-Tov 1997).

terms of diet. However, they have the ability to adapt to abundant food resources (including those from aquatic habitats) whenever they appear. Shallow inundated ponds created in the last stage of draining provide cattle egret with abundant suitable food, such as tadpoles and adults of amphibia (Ashkenazi & Dimentman 1998). Such habitats are also the preferred foraging sites of the glossy ibis. The late arrival of both species at Lake Hula may be attributed to the cultivation of the drained area of Amik Gölü, and probably to the final destruction of their breeding habitats such as stands of reeds and trees. The influx of cattle egret to the Lake Hula breeding colony is more complicated, however, as unexplained changes in their habitat in Africa probably caused their rapid spread in Europe during the 1960's (Bredin 1983). However, they joined Lake Hula later, during the last draining stages of Amik Gölü.

Inter-relations between avian populations of the Hula and el-Azraq wetlands

Most of the migrating birds that pass through el-Azraq Oasis in spring probably continue to Eastern Europe, mainly the former Soviet Union. The few ringing recoveries from the el-Azraq area support this view (Nelson 1973). There is also good evidence for an eastern migrating flyway in autumn from Europe and the western former Soviet Union to eastern and central Africa, crossing eastern Turkey and el-Azraq Oasis (Nelson 1973). Ringing recovery data indicate that wintering populations of el-Azraq ducks, such as teal, pintail, wigeon, shoveler, and garganey, originate from western and central Russia rather than the extreme east (Nelson 1973). Teal from around the Ural Mountains migrate to the western shores of the Caspian Sea and south to the Nile Delta. Pintail, after molting in the Volga Delta, migrate in several fly-lines; the southwest line reaches the Nile Delta and probably includes the el-Azraq birds. Shovelers from the Volga migrate to the Eastern Mediterranean and Egypt. One of the main migrating routes of garganey from the molting area in the Volga Delta is to Georgia, Arabia, and northeast Africa; this migrating route is probably the one seen at el-Azraq Oasis. For these birds, a severe barrier of desert and semi-desert exists between the oasis and their destination to the north or south, making the oasis a very important stopover station. After the drainage of Lake Hula and Amik Gölü, el-Azraq Oasis remained the only serious option for wildfowl in passage and wintering in the broad flyway of the Middle East between the Mediterranean and Iraq (Nelson 1973). The drainage of the oasis left this flyway without any secure foraging station. Although the desert is not a barrier for migrating ducks, one may assumed that species that need the stopover for foraging, and in particular smaller passerines that used to migrate through this area, have been forced to shift their route ca. 100 km to the west, to the Jordan Rift Valley and the Hula Valley wetlands.

Bird species that are abundant in one of the wetlands and rare in the others may provide information on the use of alternative wetlands. Shelduck used to breed in el-Azraq Oasis and were also abundant there in winter. Since the winter of 1978/79 was very dry in the region, Qa el-Azraq was not flooded and could not provide adequate food for wintering and migrating species. Hence, bird counts in el-Azraq Oasis during that winter show that only 2,500 birds were present there (Evans 1994). In the same year, winter counts of waterbirds in Israel showed an enormous increase in the number of shelduck (Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980). This species breeds mainly in Russia and was rare in Amiq Gölü, with low numbers in winter avian counts in Turkey during the early 1970's (Koning 1973). Therefore, it is assumed that this influx of shelduck to wetlands in northern Israel in 1979 was a result of the drought in Qa el-Azraq. The increase in mallards wintering in Israel in 1979 (Figure 3) should probably be attributed to the same cause.

Factors determining decline in waterbird populations

Habitat loss

The main factor that determines the presence or absence of an avian population is the availability of habitats. Resident avian populations require habitats for foraging, roosting, and breeding. Wintering and migrating populations need habitats for foraging and for roosting, in either colonial or solitary roosts. A different habitat is often required for each of these activities. Consequently, in order to harbor diverse avian populations, the site must have a certain degree of habitat diversity. The three former wetlands – Lake Hula, Amik Gölü, and el-Azraq Oasis – were extremely rich in habitats, a fact reflected in their avian population. The creation of Lake Agmon by reflooding part of the former Lake Hula provided evidence for the presence or absence of avian species according to availability of habitats (Ashkenazi & Dimentman 1998). The documentation of the avian fauna of Amik Gölü during the draining stages by Kumerloeve (1960, 1963, 1966, 1970) is of great value for following the responses of different species to loss of habitat, as demonstrated above with the group of herons.

Loss of habitat also affects food resources, which are sometimes very specific. One of the main food items of tufted duck in inland waters in Europe is the Zebra-mussel, *Dreissena polymorpha* (Olney 1963). Tufted ducks obtain *Dreissena* from the bottom by diving (ca. 2 m or more) and usually swallow the whole mollusc. Tufted ducks were recorded as wintering and breeding in large numbers in Amik Gölü (Kumerloeve 1963), and *Dreissena* was extremely abundant in the lake before its drainage (Gruvel 1931). It is suggested that tufted ducks abandoned Amik Gölü in the final stages of drainage, when populations of *Dreissena* started to decline. Thus, the unexplained 60% increase in wintering tufted ducks in northern Israel from 4,200 in 1973 to 8,600 in 1975 (Figure 3) might be attributed to the final drainage of Amik Gölü. Ducklings of tufted ducks feed mainly on molluscs, such as *Theodoxus* sp., *Bythinia* sp., and Limnaeid species (Olney 1963), that were abundant in Lake Hula before its drainage (Dimentman et al. 1992). In view of these specific food requirements, the cessation of breeding by populations of tufted ducks in Lake Hula after its drainage can be attributed to the disappearance of most of the mollusc species in the lake.

Specimen collecting and hunting

The collecting of eggs and skins of endemic avian species considered exotic by European collectors was a great threat to endangered populations. Besides the undoubted effect of the drainage, two of the resident species of Amik Gölü, Darter and Purple Gallinule, were probably affected by additional human disturbance. It is supposed that several stress factors led to the extinction of these two species even before the final drainage of the lake.

The extinction of the darter in the Levant was probably due to the combined effect of nest-robbing and the draining of Amik Gölü. Aharoni (1943) mentions that as early as the 1940's hundreds of darter eggs were collected, and several adult birds were shot on their nests for collectors in Europe, who paid large amounts of money for them. Kumerloeve (1963) confirms the presence of such large collections in European museums.

Another example is the population of the purple gallinule from Amik Gölü in Turkey, which is on the verge of extinction because of severe hunting pressure (Akçakaya 1989). The species was first described in Amik Gölü in 1911 (Aharoni 1911) and later reported in 1932 (Aharoni 1932). Amik Gölü was the main breeding site of a population that bred twice per year (Aharoni 1911). Though the population declined during the draining of the lake, hunting was one of the main threats to this species, as local hunters valued its meat (Kasparek et al. 1989).

Hunting of a single species can lead to destruction of its population, as in the case of the Pygmy Cormorant, *Phalacrocorax pygmeus*, in Lake Hula. During the 1940's there was a breeding population in the Hula swamps, but the species was exterminated by fishermen in the Hula Valley even before the drainage of the lake (Zahavi 1957; Yom-Tov & Mendelssohn 1988). The species disappeared from Israel in the 1950's but reappeared in 1982 as a wintering species in northern Israel. It has been breeding again in the Hula area since 1995 (Ashkenazi & Yom-Tov 1997).

Pesticides and poisoning

It is assumed that the main reason for the cessation of breeding by populations of grey heron, both in Amik Gölü in 1962 and in the Hula Nature Reserve in 1964, was the use of pesticides. Yom-Tov & Mendelssohn (1988) showed the very broad effect of the use of pesticides (mainly thallium sulfate) for control of rodents in Israel during the 1950's. In the case of the grey heron, the almost simultaneous ceasing of breeding in Lake Hula and Amik Gölü was probably the result of secondary poisoning through their diet, which is largely based on rodents.

The Bald Ibis, *Geronticus eremita*, is probably another victim of the use of pesticides. About 70% of the populations of this species in southeastern Turkey died during the 1950's and 1960's. Moreover, the surviving populations failed to produce any chicks until 1970, as a result of the area having been sprayed with DDT against malaria and locust swarms (Akçakaya 1989). This endemic and rare population had already suffered from egg and skin collecting by European collectors and became extinct in the wild (Akçakaya 1989).

Weather conditions

The winter of 1972 was an extremely cold one in Europe and Turkey (Dijksen et al. 1972). Populations of several wintering species in Israel, such as the little grebe, little egret, Spoonbill, *Platalea leucorodia*, Gadwall, *Anas strepera*, mallard, pintail, and tufted duck, increased by 50–500% in 1972 compared to 1971 (Suaretz, unpublished annual winter waterbird counts in Israel, 1965–1980). Species like teal, northern shoveler, shelduck, gadwall, pochard, and European coot already showed a similar increase in populations in 1971 compared to 1970. Moreover, population numbers did not drop again in 1973–1974, indicating that the weather was not the main reason for the detected increase of several populations in 1972. Rather, the increase of wintering populations in Israel should be attributed to the final stage of the draining of Amik Gölü.

Conservation implications

The deterioration of wetlands in different parts of the world, particularly in the Mediterranean region and the Middle East, accelerated during the second part of the twentieth century with the increase in demand for agricultural land. The wetlands of the Levant have undergone extensive human-induced transformation by drainage. In terms of nature conservation, loss of habitat is the most dramatic factor affecting waterbird populations. In addition to providing habitats for wintering and breeding avian populations, the Levant wetlands were the last large and diverse habitat in the migratory flyways of waterbirds before the broad belt of the desert in the south.

Drainage of large wetlands causes gradual desertion by birds as the process advances. In the final stage, the remaining waterbirds must move elsewhere and find alternative sites. The possibility of the displaced birds settling elsewhere depends on the availability of similar habitats and on the size of the alternative habitats, which are limited in their carrying capacity to a certain number of birds. In terms of nature conservation, birds that can find habitats for breeding, roosting, and foraging in the same area have a great energetic advantage over birds that have to find different sites for their specific habitat requirements.

Lake Hula was drained during a relatively short time and the rehabilitated reserve area was reconstructed almost immediately in 1958. The new site enabled continuous use of the area at least by the colonial breeding herons and other accompanying avian species. The successful rehabilitation, forty years after the drainage, of an additional area (Lake Agmon) in the north of the Hula Nature Reserve is a most welcome development for nature conservationists and scientists. The two reconstructed wetlands are used as complementary habitats by the avian populations of the Hula Valley and have enabled the reestablishment of breeding populations of at least two species that had been considered non-breeding since the drainage of Lake Hula (Ashkenazi & Dimentman 1998). However, despite this success, the reconstructed wetlands (the Hula Nature Reserve and Lake Agmon) are not large enough to meet the needs of the birds that lost their habitats in Amik Gölü, el-Azraq Oasis, or even in the former Lake Hula.

As early as the 1930's, Gruvel (1931) warned of the destructive results of the drainage plans for Amik Gölü. A call for conservation of the outstanding diverse avian fauna of the lake appeared in Kumerloeve's comprehensive work on the birds of the lake, carried out during the intensive draining stages (Kumerloeve 1963, 1966). Kence (1987) suggested a combination of agriculture with wetlands, as in the Sultansazligi wetland in Turkey, rather than complete drainage. In 1989, about ten years after the lake's final drainage, Karaca (1987) and Kumerloeve (1989) suggested reflooding of the area in order to rehabilitate parts of the former Amik Gölü and its wetlands.

A regional effort is needed to rehabilitate additional sections of the drained wetlands of Lake Hula, Amik Gölü, and el-Azraq Oasis by gradual and partial reflooding. In the Amik Valley, Göl Basi (the remaining area of the northern lake), with its seasonally inundated surroundings, must be considered the primary site for rehabilitation. In el-Azraq Oasis, allocation of greater quantities of water to the former swamp and hydrological means of retaining the floodwater of Qa el-Azraq may lead to the first steps in saving the surviving aquatic fauna and flora of the Levant.

The rate of deterioration of habitats and loss of avian species in the Levant during the last fifty years is astonishing in comparison to prehistoric data on avian species from 'Ubeidiya (Tchernov 1980), GBY (Simmons 2004), and Eynan (Pichon 1987). The darter was present in the region for more than a million years before its rapid human-induced extinction fifty years ago. It was found in the Pleistocene sites of the Upper Jordan Rift Valley, 'Ubeidiya (1.4 Ma) and GBY (0.78 Ma). Similarly, the purple gallinule survived in 'Ubeidiya, GBY, and Eynan but became extinct as a result of hunting pressure and the draining of Amik Gölü. Other species that have survived over these long periods, such as the Water Rail, *Rallus aquaticus*, European coot, Great Crested Grebe, *Podiceps cristatus*, Great Cormorant, *Phalacrocorax carbo*, shelduck, teal, and European wigeon, are probably more resistant species that have found alternative habitats to the drained areas.

This study has emphasized the avian faunal aspect of the Levant wetlands, which have gradually been destroyed. However, the most important base for supporting the avian populations is the aquatic flora and invertebrate fauna that support populations of taxa in higher trophic levels, as primary producers and primary prey. Rehabilitation of the Levant wetlands requires a regional plan that will allocate different habitats to different sites in order to create a high aquatic regional biodiversity that will attract higher taxa, such as birds. It is suggested that habitat reconstruction plans should designate the present Hula wetlands and the proposed reflooded area of Amik Gölü as larger and deeper water bodies that can support fish populations for pelicans and cormorants and can harbor wintering ducks. Large reedbeds in their surroundings would harbor breeding colonial herons and solitary reed nesters. This habitat would provide roost sites for migrating harriers, wagtails, and swallows. The planned Amik wetland with its surrounding rivers is probably the most suitable for reconstruction of pebble-bed habitats. Such habitat is very important for development of some unique aquatic invertebrates (Dimentman et al. 1992) and as a breeding site for certain plovers and terns. The unique seasonally inundated brackish water playa lake of Qa el-Azraq and parts of the inundated Amik Valley are suggested as major wintering grounds for ducks. Qa el-Azraq is important mainly for species that use the eastern flyway in migration, like the shelduck, Ruff, *Philomachus pugnax*, garganey, Yellow Wagtail, *Motacilla flava*, and swallow. It is also extremely important for several endangered desert species such as the Houbara, *Chlamydotis undulata*, and Hoopoe Lark, *Alaemon alaudipes*. In addition, it is suggested that large saline lakes and swamps should be added to this regional conservation plan. One of these is Sabkhat al-Jabbul (Jabbul Salt Lake) in Syria (Figure 1), a large shallow salt lake in a closed basin of ca. 37.5 km^2 (Evans 1994). This saline lake is important mainly for the breeding of the Greater Flamingo, *Phoenicopterus ruber*, Avocet, *Recurvirostra avosetta*, the endangered Marbled Teal, *Marmaronetta angustirostris*, and White-headed Duck, *Oxyura leucocephala* (Evans 1994).

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References

Acar, B. (1972). *Kuslarimiz*. Redhouse Yayinevi, 96 p. [Our Birds].

Aharoni, I. (1911). Am Brutplatz von *Plotus chantrei*, Oustalet. *Zeitschrift für Oologie* **1**, 33–35.

Aharoni, I. (1930). Brutbiologisches aus dem Antiochia See. *Beiträge zur Fortpflanzungsbiologie der Vögel* **6**, 145–151.

Aharoni, J. (1932). Bemerkungen und Ergänzungen zu R. Meinertzhagens Werk "Nicoll's Birds of Egypt". *Journal of Ornithology* **80**, 416–424.

Aharoni, I. (1943). *Memoirs of a Hebrew Zoologist*. Tel Aviv: "Am Oved" (in Hebrew).

Akçakaya, H. R. (1989). An overview of bird conservation in Turkey. *Sandgrouse* **11**, 52–56.

Andrews, I. J. (1995). *The Birds of the Hashemite Kingdom of Jordan*. Dundee, Scotland: Burns & Harris (Print) Limited.

Andrews, I. J. (1996). Preliminary data on raptor passage in Jordan. *Sandgrouse* **18**, 36–45.

Ashkenazi, S. & Hakham, E. (1987). *Names and Status of the Vertebrates in Israel*. Nature Conservation in Israel, Supplement **1**. Nature Reserves Authority.

Ashkenazi, S. & Yom-Tov, Y. (1997). The breeding biology of black-crowned night-heron (*Nycticorax nycticorax*) and the little egret (*Egretta garzetta*) at the Huleh Nature Reserve, Israel. *Journal of Zoology, London* **242**, 623–641.

Ashkenazi, S. & Dimentman, Ch. (1998). Foraging, nesting and roosting habitats of the avian fauna of the Agmon wetland, northern Israel. *Wetlands Ecology and Management* **6**, 169–187.

Belon, P. (1555). *Les Observations de Plusieurs Singularités et Choses Mémorables, Trouvées en Grèce, Asie, Judée, Egypte, et Autres Pays Etranger*. Anvers.

Bredin, D. (1983). *Contribution à l'Etude Ecologique d'Ardeola Ibis, Héron Gardeboeufs de Camargue*. Unpublished Ph.D. Thesis, University of Toulouse.

Burch, J. B. (1985). *Handbook on Schistosomiasis and Other Snail-mediated Diseases in Jordan.* Ann Arbor, Michigan, U.S.A. and Amman, Hashemite Kingdom of Jordan.

Cameron, R. A. D. & Cornwallis, L. (1966). Autumn notes from Azraq, Jordan. *Ibis* **108**, 284–287.

Clarke, J. E. (1980). The avifauna of Shaumari Wildlife Reserve. *Sandgrouse* **1**, 50–70.

Conder, P. (1981). Birds of the Azraq Wetland Reserve, Jordan: January and February 1979. *Sandgrouse* **2**, 22–32.

Dijksen, L. J., Koning, F. J. & Walmsley, J. G. (1972). *I.W.R.B. Mission to Turkey, Winter 1971–1972*. Report, 22 p.

Dimentman, Ch., Bromley, H. J. & Por, F. D. (1992). *Lake Hula*. Jerusalem: The Israel Academy of Sciences and Humanities.

Evans, M. I. (1994). *Important Bird Areas in the Middle East*. Birdlife International, Birdlife Conservation Series **2**, 410 pp.

Garcia-Orcoyen Tormo, C., Vallecillo, C. G. & Valladares, M. A. (1992). How many inland Mediterranean wetlands will there be in the year 2000? *IWRB Special Publication* **20**, 28–31.

Garrard, A. N., Colledge, S., Hunt, C. & Montague, R. (1989). Environment and subsistence during the Late Pleistocene and early Holocene in the Azraq Basin. *Paléorient* **14**, 40–49.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–947.

Grimmett, R. F. A. & Jones, T. A. (1989). *Important Bird Areas in Europe.* International Council for Bird Preservation, European Continental Section. ICBP Technical Publication **9**, Turkey, pp. 707–741.

Gruvel. A. (1931). *Les États de Syrie, Richesses Marines et Fluviales Exploitation Actuelle - Avenir.* Bibliothèque de la Faune des Colonies Françaises. Paris: Société d'Éditions

Geographiques, Maritimes et Coloniales.

Hambright, K. D. & Zohary, T. (1988). Lakes Hula and Agmon: Destruction and creation of wetland ecosystems in northern Israel. *Wetlands Ecology and Management* **6**, 83-89.

Hardy, E. (1946). *A Handlist of the Birds of Palestine*. Education Officer, G. H. Q., Middle East Forces. 49 pp.

Harrison, D. L. & Bates, P. J. J. (1991). *The Mammals of Arabia*. Harrison Zoological Museum.

Hollom, P. A. D. (1959). Notes from Jordan, Lebanon, Syria and Antioch. *Ibis* **101**, 183–200.

Hovel, H. (1987). *Check-list of the Birds of Israel*. Tel Aviv: Tel Aviv University and the Society for the Protection of Nature in Israel.

Karaca, H. (1987). Amik Gölünün kurutulmasi faydadan çok ziyan getirdi. *AV* **18**, 1 [Draining of Amik Gölü caused more damage than benefit].

Karmon, Y. (1953). The settlement of the Northern Huleh Valley since 1838. *Israel Exploration Journal* **3**, 4–25.

Karmon, Y. (1960). The drainage of the Huleh swamps. *Geographical Review* **50**, 169–196.

Kasparek, M. (1992). *Die Vögel der Türkei eine Übersicht*. Heidelberg, Germany: Verlag.

Kasparek, M., Bilgin, C. C. & Akin, A. (1989). The Purple Gallinule, *Porphyrio porphyrio*, in the Eastern Mediterranean. *Zoology in the Middle East* **3**, 19–30.

Kence, A. (1987). *Biological Diversity in Turkey*. Ankara: Environmental Problems Foundation of Turkey.

Khoury, F. (1996). Observations on the avifauna of the Azraq wetland, Jordan, June 1995. *Sandgrouse* **18**, 52–57.

Koning, F. J. (1973). Quantitative angaben über die in der Türkey überwinternden Anatiden. *Bonn. Zol. Beitr.* **24**, 219–226.

Krupp, F. (1985a). *Barbus chantrei* (Sauvage 1882), a valid species of cyprinid fish from the northern Levant (Pisces: Osteichthyes: Cyprinidae). *Senckenbergiana Biol.* **66**, 17–25.

Krupp, F. (1985b). Rehabilitation of *Barbus lorteti* Sauvage, 1882, and comments on the validity of the generic names *Bertinius* Fang, 1943, and *Bertinichthys* Whitley, 1953 (Pisces: Cyprinidae). *Hydrobiologia* **120**, 63–68.

Krupp, F. & Schneider, W. (1989). The fishes of the Jordan River drainage basin and Azraq Oasis. *Fauna of Saudi Arabia* 10, 347-416.

Kumerloeve, H. (1960). Zur Verbreitung des Rallenreihers *Ardeola ralloides* (Scop.), in Vorderasien. *Acta Ornithologica* **5**, 301–306.

Kumerloeve, H. (1963). L'avifaune du Lac d'Antioche (Amiq Gölü - Göl Basi) et de ses alentours. *Alauda* **31**, 110–136, 161-211.

Kumerloeve, H. (1964). Zur Sumpf- und Wasservogelfauna der Türkei. *Journal of Ornithology* **105**, 307–308.

Kumerloeve, H. (1966). Migration et hivernage sur le Lac d'Antioche (Amik Gölü, Hatay, Turquie). Coup d'oeil sur son avifaune nidificatrice actuelle. *Alauda* **34**, 299–308.

Kumerloeve, H. (1969). Recherches sur l'avifaune de la République Arabe Syrienne, essai d'un aperçu. *Alauda* **37**, 43–58, 114–134, 188–205.

Kumerloeve, H. (1970). Zur Kenntnis der Avifauna Kleinasiens und der europäischen Türkei. *Istanbul Üniversitesi Fen Fakültesi Mecmuasi*, Ser. **B35**, 85–160.

Kumerloeve, H. (1984). A chronological review of birds first described from Turkey with their current taxonomic status in 1984. *Sandgrouse* **6**, 62–68.

Kumerloeve, H. (1989). Amik Gölü, south-east Turkey: A plea for national park status. *OSME Bulletin* **23**, 5–6.

Kuru, M. (1987). Freshwater fauna. In (A. Kence, Ed.) *Biological Diversity in Turkey*. Ankara: Environmental Problems Foundation of Turkey, pp. 129–140.

Locard, A. (1883). *Malacologie des Lacs de Tibériade d'Antioche et d'Homs*. Lyon: Libraire de la Faculté de Médecine et de la Faculté de Droit.

Lortet, L. (1883). *Etudes Zoologiques Sur la Faune du Lac de Tibériade, Suivies d'un Aperçu Sur la Faune des Lacs d'Antioche et de Homs*. Archives du Muséum d'Histoire Naturelle de Lyon III, pp. 99–109.

Magnin, G. & Yarar, M. (1997). *Important Bird Areas in Turkey*. Istanbul: Doğal Hayati Koruma Dernesi.

Meinertzhagen, R. (1935). Ornithological results of a trip to Syria and adjacent countries in 1933. *Ibis* **13**, 110–151.

Merom, H. (1960). *The Birds of Israel*. Tel Aviv: Hakibbutz Hameuchad (in Hebrew).

Mountfort, G. (1966). *Portrait of a Desert, the Story of an*

Expedition to Jordan. London: Collins.

Nelson, B. (1985). Return to Azraq. *Oryx* **19**, 22–26.

Olney, P. J. S. (1963). The food and feeding habits of the Tufted Duck *Aythya fuligula*. *Ibis* **105**, 55–62.

Papayannis, T. (1992). Wetland degradation at Ramsar sites in the Mediterranean. In (M. Finlayson, T. Hollis & T. Davis, Eds.) *Managing Mediterranean Wetlands and Their Birds*, *IWRB Special Publication* **20**, 97–105.

Paz, U. (1976). *The Rehabilitation of the Huleh Reserve*. Tel Aviv: Israel Nature Reserves Authority.

Pichon, J. (1987). L'avifaune. In (J. Bouchud, Ed.) *La Faune du Gisement Natoufien de Mallaha (Eynan), Israel.* Mémoires et Travaux de Centre de Recherche Français de Jérusalem **4**, Jerusalem: Association Paléorient, pp. 115–150.

Por, F. D. & Dimentman, Ch. (1989). *The Legacy of Tethys, an Aquatic Biogeography of the Levant*. Monographiae Biologicae **63**. Dordrecht: Kluwer Academic Publishers.

Scates, M. D. (1968). Notes on the hydrobiology of Azraq Oasis Jordan. *Hydrobiologia, Acta Hydrobiologica Hydrographica et Protistologica* **31**, 73–80.

Schütt, H. (1993). Die gattung *Dreissena* im Quartar Anatoliens (Bivalvia: Eulamellibranchiata: Dreissenacea). *Archiv für Molluskenkunde* **122**, 323–333.

Simmons, T. (2004). "A feather for each wind that blows": Utilizing avifauna in assessing changing patterns in palaeoecology and subsistence at Jordan Valley archeological sites. In: (N. Goren-Inbar & J. D. Speth, Eds.) *Human Paleoecology in the Levantine Corridor*. Oxford: Oxbow Books, pp. 191–205.

Smith, G. A. (1973). *The Historical Geography of the Holy Land*. London: Collins.

Suaretz, S. & Paz, U. (1975). Heron breeding colonies in Israel. *Nature Conservation in Israel. Research and Survey* **1**, 43–94 (in Hebrew).

Tchernov, E. (1980). *The Pleistocene Birds of 'Ubeidiya, Jordan Valley*. Jerusalem: Israel Academy of Sciences and Humanities.

The General Corporation for the Environment Protection. (1998). *Jordan Country Study on Biological Diversity*. The Hashemite Kingdom of Jordan, The General Corporation for the Environment Protection, UNDP and UNEP, 416 p.

Tristram, H. B. (1882). Ornithological notes of a journey through Syria, Mesopotamia, and Southern Armenia in 1881. *Ibis* **6**, 402–419.

Valla, F. R. (1995). The first settled societies – Natufian (12,500–10,200 BP). In (T. E. Levy, Ed.) *The Archaeology of Society in the Holy Land*. London: Leichester University Press, pp. 169–189.

Varisligil, A. (1968). The over-all problems of wetlands in Turkey, with special reference to use and legislation. *IUCN Publications* **12**, 51–57.

Wallace, D. I. M. (1982). Observations on migrant birds at Azraq in north-east Jordan, up to April 1967. *Sandgrouse* **4**, 77–99.

Wallace, D. I. M. (1983). The breeding birds of the Azraq Oasis and its desert surround, Jordan, in the mid-1960s. *Sandgrouse* **5**, 1–18.

Wallace, D. I. M. (1984). Selected observations from Lebanon, Syria and Jordan in the springs of 1963 and 1966. *Sandgrouse* **6**, 24–47.

Yom-Tov, Y. & Mendelssohn, H. (1988). Changes in the distribution and abundance of vertebrates in Israel during the 20th century. In (Y. Yom-Tov & E. Tchernov, Eds.) *The Zoogeography of Israel*. Dordrecht, The Netherlands: Dr. W Junk Publishers, pp. 515–547.

Zahavi, A. (1957). The breeding birds of the Huleh Swamp and Lake (Northern Israel). *Ibis* **99**, 600–607.

Zalles, J. I. & Bildstein, K. L. (2000). *Raptor Watch: A Global Directory of Raptor Migration Sites*. Birdlife International, Birdlife Conservation **9**, 117–203.

Zohary, M. & Orshanski, G. (1947). The vegetation of the Huleh Plain. *Palestine Journal of Botany , Jerusalem Series* **4**, 90–104.

Appendix. Avian species recorded in the former wetlands of the Levant.

Scientific Name	**Common Name**	**Lake Hula**	**Amik Gölü**	**El-Azraq Oasis**
*Tachybaptus ruficollis**	Little Grebe	B	B	B
*Podiceps cristatus** (-)	Great Crested Grebe	B	B	+
*Podiceps grisegena**	Red-necked Grebe	+		
*Podiceps nigricollis**	Black-necked Grebe	B ?		
*Phalacrocorax carbo**	Great Cormorant	+	B	+
*Phalacrocorax pygmeus**	Pygmy Cormorant	B	B	
*Anhinga rufa chantrei** (-)	Pennant Darter	+	B	
*Pelecanus onocrotalus**	Great White Pelican	B ?	B	+
*Pelecanus crispus**	Dalmatian Pelican	B ?	B	
*Botaurus stellaris**	Bittern	+	+	+
*Ixobrychus minutus**	Little Bittern	B	B	B
*Nycticorax nycticorax**	Black-crowned Night-heron	+	B	+
*Ardeola ralloides**	Squacco Heron	B ?	B	B
Bubulcus ibis	Cattle Egret	+	B	+
*Egretta garzetta**	Little Egret	B	B	+
*Egretta alba**	Great White Egret	+	B	+
*Ardea cinerea** (-)	Grey Heron	B	B	+
*Ardea purpurea**	Purple Heron	B	B	B
*Ardea goliath**	Goliath Heron	+		
*Mycteria ibis**	Yellow-billed Stork		+	
*Ciconia nigra**	Black Stork			+
*Ciconia ciconia**	White Stork	+	+	+
*Plegadis falcinellus**	Glossy Ibis	B	B	+
Geronticus eremita	Bald Ibis		+	
*Platalea leucorodia**	Spoonbill	+	B	+
*Phoenicopterus ruber**	Greater Flamingo	+	+	+
*Cygnus olor**	Mute Swan			+
*Anser albifrons**	White-fronted Goose	+		+
*Anser anser**	Grey-lag Goose	+		+
*Tadorna ferruginea**	Ruddy Shelduck	+	+	+
*Tadorna tadorna**	Shelduck	+	+	B
*Anas penelope**	European Wigeon	B ?	B ?	+
*Anas strepera**	Gadwall	+	B ?	+
*Anas crecca**	Teal	+	B	B
*Anas falcata**	Falcated Teal			+
*Anas platyrhynchos**	Mallard	B	B	B
*Anas acuta**	Pintail	+	+	B
*Anas querquedula**	Garganey	B ?	+	B
*Anas clypeata**	Northern Shoveler	+	+	+
*Marmaronetta angustirostris**	Marbled Teal	B	B	+
*Netta rufina**	Red-crested Pochard	+	B	+
*Aythya ferina**	Pochard	+	+	+
*Aythya nyroca**	Ferruginous Duck	B	B	+
*Aythya fuligula**	Tufted Duck	+	B	+
*Aythya marila**	Greater Scaup	+		
*Melanitta fusca**	Velvet Scoter	+		
*Bucephala clangula**	Goldeneye	+		+
*Mergus albellus**	Smew			+
*Mergus serrator**	Red-breasted Merganser			+
*Oxyura leucocephala** (-)	White-headed Duck	B	B ?	
Pernis apivorus	Honey Buzzard		+	+
Milvus migrans	Black Kite			+
*Haliaeetus albicilla** (-)	White-tailed Eagle	B	B	

Scientific Name	Common Name	Lake Hula	Amik Gölü	El-Azraq Oasis
Neophron percnopterus	Egyptian Vulture		+	+
Gyps fulvus	Griffon Vulture		+	+
Torgos tracheliotus	Lappet-faced vulture			+
Circaetus gallicus	Short-toed Eagle		B	+
*Circus aeruginosus** (-)	Marsh Harrier	B	B	B
*Circus cyaneus**	Hen Harrier			+
Circus macrourus	Pallid Harrier			+
*Circus pygargus**	Montagu's Harrier		+	+
Accipiter gentilis	Goshawk			+
Accipiter nisus	Sparrowhawk			+
Accipiter brevipes	Levant Sparrowhawk			+
Buteo buteo	Buzzard			+
Buteo rufinus	Long-legged Buzzard			+
Buteo lagopus	Rough-legged Buzzard			+
Aquila pomarina	Lesser-spotted Eagle	+	+	+
Aquila clanga (-)	Spotted Eagle	B		+
Aquila rapax	Tawny Eagle			+
Aquila heliaca	Imperial Eagle		+	+
Aquila chrysaetos	Golden Eagle		+	+
Hieraaetus pennatus	Booted Eagle		+	+
Hieraaetus fasciatus	Bonelli's Eagle		+	
*Pandion haliaetus**	Osprey	+		+
Falco naumanni	Lesser Kestrel		B	+
Falco tinnunculus	Kestrel		+	B
Falco vespertinus	Red-footed Falcon		+	+
Falco columbarius	Merlin		+	
Falco subbuteo	Hobby		+	+
Falco biarmicus	Lanner			+
Falco cherrug	Saker			+
Falco peregrinus	Peregrine		+	+
Alectoris chukar	Chukar		+	B
Ammoperdix heyi	Sand Partridge			B
*Francolinus francolinus**	Black Francolin	+	+	
Coturnix coturnix	Common Quail		+	+
*Rallus aquaticus**	Water Rail		B	B
*Porzana porzana**	Spotted Crake		B ?	+
*Porzana parva**	Little Crake			+
*Porzana pusilla** (-)	Baillon's Crake	B		B
*Crex crex**	Corn Crake			+
*Gallinula chloropus**	Moorhen	B	B	B
*Porphyrio porphyrio** (-)	Purple Gallinule	B	B	
Fulica atra * (-)	European Coot	B	B	+
*Grus grus**	Common Crane	+		+
Chlamydotis undulata	Houbara		+	B
*Haematopus ostralegus**	Old-World Oystercatcher			+
*Himantopus himantopus**	Black-winged Stilt	B	B	B
*Recurvirostra avosetta**	Avocet		+	B
Burhinus oeducnemus	Stone Curlew			B
Cursorius cursor	Cream-coloured Courser			B
*Glareola pratincola**	Pratincole	B	B	B
*Glareola nordmanni**	Black-winged Pratincole		+	
*Charadrius dubius** (-)	Little Ringed Plover	B	B ?	B
*Charadrius hiaticula**	Ringed Plover		+	+
*Charadrius alexandrinus**	Kentish Plover	+	B	B

Scientific Name	Common Name	Lake Hula	Amik Gölü	El-Azraq Oasis
*Charadrius leschenaultii**	Greater Sand Plover		+	B
*Charadrius asiaticus**	Caspian Plover		+	+
*Pluvialis apricaria**	Golden Plover		+	
*Hoplopterus spinosus**	Spur-winged Lapwing	B	B	B
*Chettusia gregaria**	Sociable Lapwing		+	+
*Chettusia leucura**	White-tailed Lapwing		+	B
Vanellus vanellus	Lapwing		+	+
*Calidris canutus**	Knot			+
*Calidris alba**	Sanderling			+
*Calidris minuta**	Little Stint	+	+	+
*Calidris temminckii**	Temminck's Stint	+		+
*Calidris ferruginea**	Curlew Sandpiper			+
*Calidris alpina**	Dunlin			+
*Limicola falcinellus**	Broad-billed Sandpiper			+
*Philomachus pugnax**	Ruff	+		+
*Lymnocryptes minimus**	Jack Snipe	+	+	+
*Gallinago gallinago**	Common Snipe	+	+	+
*Gallinago media**	Great Snipe		+	+
Scolopax rusticola	Eurasian Woodcock		+	+
*Limosa limosa**	Black-tailed Godwit	+		+
*Limosa lapponica**	Bar-tailed Godwit			+
*Numenius phaeopus**	Whimbrel			+
*Numenius arquata**	Eurasian Curlew	+	+	+
*Tringa erythropus**	Spotted Redshank	+	+	+
*Tringa totanus**	Redshank	+	+	+
*Tringa stagnatilis**	Marsh Sandpiper		+	+
*Tringa nebularia**	Greenshank	+	+	+
*Tringa ochropus**	Green Sandpiper	+	+	+
*Tringa glareola**	Wood Sandpiper	+	+	+
*Xenus cinereus**	Terek Sandpiper			+
*Actitis hypoleucos**	Common Sandpiper	+	+	+
*Arenaria interpres**	Turnstone	+	+	+
*Phalaropus lobatus**	Red-necked Phalarope			+
*Larus minutus**	Little Gull	+		
*Larus ridibundus**	Black-headed Gull	+	+	+
*Larus genei**	Slender-billed Gull		+	+
*Larus canus**	Common/Mew Gull		+	
*Larus fuscus**	Lesser Black-backed Gull		+	+
*Larus argentatus**	Herring Gull	+	+	
*Gelochelidon nilotica**	Gull-billed Tern		+	B
*Sterna bengalensis**	Lesser Crested Tern	+		
*Sterna sandvicensis**	Sandwich Tern			+
*Sterna hirundo**	Common Tern	B	B	+
*Sterna paradisaea**	Arctic Tern			+
*Sterna albifrons** (-)	Little Tern	B	B	B
*Chlidonias hybridus** (-)	Whiskered Tern	B	+	+
*Chlidonias niger** (-)	Black Tern	B	B	+
*Chlidonias leucopterus**	White-winged Black Tern	+	+	+
Pterocles senegallus	Spotted Sandgrouse			B
Pterocles orientalis	Black-bellied Sandgrouse		+	B
Pterocles alchata	Pin-tailed Sandgrouse			B
Columba livia	Rock Dove		+	B
Columba palumbus	Wood Pigeon	+		+
Streptopelia decaocto	Collared Dove		B	

Scientific Name	**Common Name**	**Lake Hula**	**Amik Gölü**	**El-Azraq Oasis**
Streptopelia turtur	Turtle Dove	B	B	+
Oena capensis	Long-tailed Dove			+
Clamator glandarius	Great Spotted Cuckoo			+
Cuculus canorus	Cuckoo		+	+
Tyto alba	Barn Owl		+	+
Otus brucei	Striated Scops Owl			+
Otus scops	Scops Owl		B ?	+
Bubo bubo	Eagle Owl		+	+
Athene noctua	Little Owl		+	B
Asio otus	Long-eared Owl			+
Asio flammeus	Short-eared Owl			+
Caprimulgus nubicus	Nubian Nightjar			+
Caprimulgus europaeus	Nightjar		+	+
Caprimulgus aegyptius	Egyptian Nightjar			B
Apus apus	Swift		+	+
Apus pallidus	Pallid Swift		+	+
Apus melba	Alpine Swift		+	+
Apus affinis	Little Swift			+
*Halcyon smyrnensis**	White-breasted Kingfisher	B	B	+
*Alcedo atthis**	Kingfisher	+	B ?	+
*Ceryle rudis**	Pied Kingfisher	B	B	+
Merops superciliosus	Blue-cheeked Bee-eater		B	B
Merops apiaster	Bee-eater		B	B
Coracias garrulus	Roller		B	+
Upupa epops	Hoopoe		+	+
J ynx torquilla	Wryneck			+
Eremalauda dunni	Dann's Lark			B
Ammomanes cincturus	Bar-tailed Desert Lark			B
Ammomanes deserti	Desert Lark			B
Alaemon alaudipes	Hoopoe Lark			B
Ramphocoris clotbey	Thick-billed Lark			B
Calandrella cinerea	Red-capped Lark		B	B
Calandrella rufescens	Lesser Short-toed Lark			B
Calandrella brachydactyla	Short-toed Lark		+	B
Galerida cristata	Crested Lark			B
Melanocorypha calandra	Calandra Lark		B	+
Melanocorypha bimaculata	Bimaculated Lark		+	+
Alauda arvensis	Skylark			+
Eremophila bilopha	Temminck's Horned Lark			B
Riparia riparia	Sand Martin		B	B
Ptyonoprogne fuligula	African Rock Martin			+
Ptyonoprogne rupestris	Crag Martin			+
Hirundo rustica	Swallow		B	+
Hirundo daurica	Red-rumped Swallow		B	+
Delichon urbica	House Martin		+	+
Anthus novaeseelandiae	Richard's Pipit			+
Anthus campestris	Tawny Pipit			B
Anthus trivialis	Tree Pipit			+
Anthus pratensis	Meadow Pipit			+
Anthus cervinus	Red-throated Pipit		+	+
*Anthus spinoletta**	Water Pipit		+	+
*Motacilla flava**	Yellow Wagtail			B
*Motacilla flava feldegg**	Black-headed Yellow Wagtail	B	B	
*Motacilla citreola**	Yellow-headed Wagtail			+

Scientific Name	**Common Name**	**Lake Hula**	**Amik Gölü**	**El-Azraq Oasis**
*Motacilla cinerea**	Grey Wagtail			+
*Motacilla alba** (-)	White Wagtail	B	B	+
Pycnonotus barbatus	Common Bulbul		+	
Cercotrichas galactotes	Rufous Bush Chat			B
Erithacus rubecula	Robin			+
*Luscinia luscinia**	Thrush Nightingale			+
Luscinia megarhynchos	Nightingale			+
*Luscinia svevica**	Bluethroat	+		+
Irania gutturalis	White-throated Robin			+
Phoenicurus ochruros	Black Redstart			+
Phoenicurus phoenicurus	Redstart			+
Saxicola rubetra	Whinchat			+
Saxicola torquata	Stonechat			+
Oenanthe isabellina	Isabelline Wheatear			B
Oenanthe deserti	Desert Wheatear		+	B
Oenanthe finschii	Finsch’s Wheatear		B	+
Oenanthe moesta	Tristram’s Wheatear			B
Oenanthe xanthoprymna	Red-tailed Wheatear			+
Oenanthe oenanthe	Wheatear		+	+
Oenanthe hispanica	Black-eared Wheatear		B	B
Oenanthe lugens	Mourning Wheatear			B
Monticola saxatilis	Rock Thrush			+
Monticola solitarius	Blue Rock Thrush			+
Turdus merula	Blackbird		+	+
Turdus philomeles	Song Thrush		+	+
Turdus viscivorus	Mistle Thrush			+
*Cettia cetti**	Cetti’s Warbler	B		
Cisticola juncidis	Fan-tailed Warbler	B	+	B
Prinia gracilis	Striped-backed Prinia	B	B	B
Scotocerca inquieta	Streaked Scrub Warbler			B
*Locustella fluviatilis**	River Warbler			+
*Locustella luscinioides**(-)	Savi’s Warbler	B	B	B
*Acrocephalus melanopogon**	Moustached Warbler	B	B	B
*Acrocephalus paludicola**	Aquatic Warbler			+
*Acrocephalus schoenobaenus**	Sedge Warbler	+		B
*Acrocephalus palustris**	Marsh Warbler		B	B
*Acrocephalus scirpaceus**	Reed Warbler	B	B	B
*Acrocephalus stentoreus**	Clamorous Great Reed Warbler	B		B
*Acrocephalus arundinaceus**	Great Reed Warbler	B	B	B
Hippolais pallida	Olivaceous Warbler			+
Hippolais caligata	Booted Warbler			+
Hippolais languida	Upcher’s Warbler		+	+
Hippolais olivetorum	Olive-tree Warbler			+
Hippolais icterina	Icterine Warbler			+
Sylvia cantillans	Subalpine Warbler			+
Sylvia mystacea	Menetries’s Warbler		+	+
Sylvia melanocephala	Sardinian Warbler		B	B
Sylvia rueppelli	Ruppell’sWarbler		+	
Sylvia nana	Desert Warbler			+
Sylvia nisoria	Barred Warbler		+	+
Sylvia curruca	Lesser Whitethroat		+	+
Sylvia communis	Common Whitethroat		+	+
Sylvia borin	Garden Warbler		+	+
Sylvia atricapilla	Blackcap		B ?	+

Scientific Name	Common Name	Lake Hula	Amik Gölü	El-Azraq Oasis
Phylloscopus bonelli	Bonelli's Warbler			+
Phylloscopus sibilatrix	Wood Warbler			+
Phylloscopus neglectus	Plain Willow Warbler			+
Phylloscopus collybita	Chiffchaff	+		+
Phylloscopus trochilus	Willow Warbler		+	+
Muscicapa striata	Spotted Flycatcher		+	+
Ficedula parva	Red-breasted Flycatcher	+		+
Ficedula albicollis	Collard Flycatcher			+
Ficedula hypoleuca	Pied Flycatcher			+
Parus major	Great Tit		+	
*Panurus biarmicus kosswigi**	Bearded Tit	+	B	
Sitta neumayer	Neumayer's Nuthatch		+	
*Remiz pendulinus**	Penduline Tit	+	B	
Oriolus oriolus	Golden Oriole		+	+
Lanius isabellinus	Isabelline Shrike			+
Lanius collurio	Red-backed Shrike		B	+
Lanius minor	Lesser Grey Shrike		+	+
Lanius excubitor	Great Grey Shrike			B
Lanius senator	Woodchat Shrike	+	B	+
Lanius nubicus	Masked Shrike	+		+
Corvus corone	Carrion Crow		B	
Corvus ruficollis	Brown-necked Raven			B
Corvus corax	Raven			B
Sturnus vulgaris	Starling		B ?	+
Sturnus roseus	Rose-coloured Starling		B	+
Passer domesticus	House Sparrow		B	B
Passer hispaniolensis	Spanish Sparrow		B	+
Petronia brachydactyla	Pale Rock Sparrow			B
Fringilla coelebs	Chaffinch			+
Carduelis chloris	Greenfinch		+	+
Carduelis carduelis	Goldfinch		+	B
Carduelis cannabina	Linnet		+	
Bucanetes githagineus	Trumpeter Finch			B
Carpodacus erythrinus	Common Rosefinch			+
Emberiza striolata	House Bunting			+
Emberiza cineracea	Cinerous Bunting			+
Emberiza hortulana	Ortolan Bunting		+	+
Emberiza caesia	Cretzschmar's Bunting		+	+
Emberiza aureola	Yellow-breasted Bunting			+
*Emberiza schoeniclus**	Reed Bunting	+	B	
Emberiza melanocephala	Black-headed Bunting		B	+
Miliaria calandra	Corn Bunting		+	

Bird nomenclature from Ashkenazi & Hakham (1987).

Data based on:

Lake Hula – Tristram 1882; Meinertzhagen 1935; Hardy 1946; Zahavi 1957; Merom 1960; Suaretz & Paz 1975; Paz 1976; Hovel 1987; Dimentman et al. 1992.

Amik Gölü – Aharoni 1911, 1930, 1932; Gruvel 1931; Hollom 1959; Kumerloeve 1960, 1964, 1966, 1970, 1984; Kasparek et al. 1989.

El-Azraq Oasis – Hollom 1959; Cameron & Cornwallis 1966; Nelson 1973, 1985; Clarke 1980; Conder 1981; Wallace 1982, 1983; Evans 1994; Andrews 1995.

Key:
Recorded breeding B
Probably breeding B ?
Observed in the site +
Water-associated *
Ceased breeding after drainage of Lake Hula (-)

Chapter XIII

"A Feather for Each Wind that Blows": Utilizing Avifauna in Assessing Changing Patterns in Paleoecology and Subsistence at Jordan Valley Archaeological Sites

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Abstract

Using both new and previously published data from the archaeological record of avifauna, this paper presents a review of changing paleoenvironmental conditions in the Jordan Valley from 1.4 million years ago to approximately 7,000 years ago. Site seasonality, human exploitation of micro-habitats, and human subsistence preferences are examined, both diachronically and synchronically when data from more than one site is available for a given time period. The prevailing pattern of bird exploitation in the Jordan Valley throughout prehistory relies heavily on the peak in bird populations brought about by the annual arrival of wintering waterfowl, and supplemented by the southerly autumn and northerly spring migrations through the rift. Habitat information confirms that during most archaeological periods people were heavily dependent on aquatic species, with those of shoreline, grasslands, and woodlands assuming far less importance. Habitat specificity of particular taxa (e.g., the requirement of deep water for fishing by the darter, *Anhinga rufa*) can further the understanding of relatively small shifts in micro-environments, such as lake level. The preference of birds for specific habitats and human exploitation of those birds (e.g., the chukar or rock partridge, *Alectoris chukar*) also allows the avifaunal record to reflect accurately the fluctuation of the desert belt in the Jordan Valley. Avifaunal data indicate that, while sedentism may have its roots in the Natufian, year-round exploitation of birds is not evident in the archaeological record until the Pre-Pottery Neolithic A. The birds of this period also reflect the fragmentation of the environment and its exploitation by an expanding population, which was thus forced into a shrinking habitable geographic area.

Introduction

While climatic shifts in the Jordan Valley from the Middle Pleistocene through the Holocene have been well documented, relatively few researchers (e.g., Tchernov 1962, 1991, 1993) have utilized the extensive avifaunal record to examine the changing paleoecology of this important region. Skeletal remains of birds are quite abundant at many Jordan Valley sites and, when identified to taxon, can provide environmental information concerning lake level, micro-environment, and seasonality. Avifaunal data can also inform about human ecology, in particular site seasonality, seasonal round and degree of sedentism. Shifts in the human exploitation of birds can also be traced though a detailed analysis of patterns of species preference and body part use over time.

The avian species recovered from archaeological sites conform to the five categories of birds classified in Israel today (Paz 1987): residents (91 species), summer residents or breeders (72 species), winter residents (94 species), passage migrants (121 species), and accidentals (127 species). As the primary migratory seasons are autumn and spring, the vast majority of birds can been seen in Israel between September/October and March/April. The passage migrants and winterers combined equal some 215 species and most of the sightings of accidental species also occur during the migratory seasons, rather than during the summer months. Hence, the profile of birds in Israel, and in the Jordan Valley in particular, is heavily biased toward the peak months between September and April. Between May and August, the bird population is reduced to 163 species. Caution is therefore warranted when interpreting the seasonal profile of a site based on the number of avian taxa represented; a peak in the number of bird species present during the winter does not necessarily indicate an occupation that took place solely or even primarily during the winter. The peak may be a normal facet of the migratory nature of the bird population in the Jordan Valley. It may, of course, also reflect the natural tendency of humans to exploit these migratory and wintering fowl at times when they are present in greatest numbers.

The Jordan Valley serves as the major migration route for European bird species wintering in the Levant and Africa, with some species using the Rift Valley route in both their southern and northern passages, while others travel through this region uni-directionally, utilizing the alternate Gibraltar route for the other. Because these migration patterns are well documented, constant, and unique to each species, the presence of a single avian taxon or certain combinations of taxa in an archaeological site can signify its occupation during a particular month or months of the year. An example of this is the buzzard (*Buteo buteo*). This species' southern migration does not pass through the Jordan Valley, but its northward migration from Africa causes it to pass through the region only during the months of March and April each year (Paz & Eshbol 1992). Other birds, such as the steppe eagle (*Aquila rapax*), migrate annually through the Jordan Valley in both directions, but at precise times (for *A. rapax* only in the months of February and October). Thus, if remains of both *Buteo buteo* and *Aquila rapax* are found on an archaeological site, one could conservatively assert that, because their coincidence is most likely to occur in the early spring (late February and early March), the human habitation of the site had to encompass at least those months.

Some avian species are also very specific with regard to habitat preference, for feeding, nesting, and raising their young. Ground-nesting birds may prove an easier resource to exploit during their brooding season, and the pre-fledged birds and fledglings would likely prove easier to take than fully adult flighted birds. While no bones of immature birds have been documented for Jordan Valley archaeological sites, this may be related to the porous nature of immature avian skeletal elements and taphonomic processes affecting their preservation. Given the fully adult nature of all avian remains recovered from the archaeological sites included in this study, I have chosen to examine the "preferred habitat" of the birds (the habitat in which they are most frequently observed) in order to reconstruct the habitat distribution (micro-environments) and the paleoecological conditions surrounding the sites. By diachronically examining the habitat preference of all taxa (both generalists and specialists) on these sites, a reconstruction of habitat distribution through time can be accomplished. The advance and retreat of lakes affecting water levels, as well as the drying of the environment and the expansion of arid zones, can be thus documented through the avifauna. This is not, of course, a direct measure of the percentage of the environment comprised by each type of habitat, although it is certainly indicative that these habitats were within the "radius of exploitation" of the residents of these sites. Rather, the habitat distribution of birds reflects a measure of the degree to which the inhabitants of various sites used each zone and considered its resources relevant to their subsistence (and other) needs.

Avian habitat preference may also reflect the changing environment. For example, it is not surprising that water and shore species dominate the avian assemblage at sites situated on lake margins. However, even when the existence of bodies of water is demonstrated archaeologically by the presence of large numbers of wintering water fowl, changes in the environment may be witnessed according to how many taxa are taken from different environments over time. A site where the vast majority of birds are water birds probably indicates the existence of a good-sized lake, whereas a site where birds are taken from a variety of environments may indicate not only that the lake is shrinking but that the relevant environmental resources are becoming more fragmented throughout the landscape. As a result, people may be exploiting different micro-environmental zones, which may also have shifted closer to the site due to climatic change. Some avian species (e.g., the darter, *Anhinga rufa*) require a particular water depth for fishing; thus, changes in lake level may also be reflected by the fluctuating presence and absence of these species at a particular site (or sites) through time.

Materials and methods

Both published data and original, previously unpublished data from ten Jordan Valley sites are presented here. These sites range in age from the 1.4-million-year-old Lower Paleolithic site of ʻUbeidiya to the ca. 7,000-year-old Pre-Pottery Neolithic A (PPNA) sites of Gilgal, Netiv Hagdud, Salabiya IX, and Ain Darat. Cultural ages of the sites and sample numbers are shown in Tables 1 and 2; the location of each site is indicated in Figure 1. As the avifaunal remains identified thus far from the recent excavations at the Middle Paleolithic site of Amud Cave are too few to be included in any analysis, the taxonomic identification of these 6 bones and the preferred habitat of the taxa are presented in Table 3. It is worthy of note, however, that none of the Amud birds are cave-dwelling species. Thus, while other predators such as small carnivores and owls may be responsible for their deposition, the Neanderthal inhabitants may

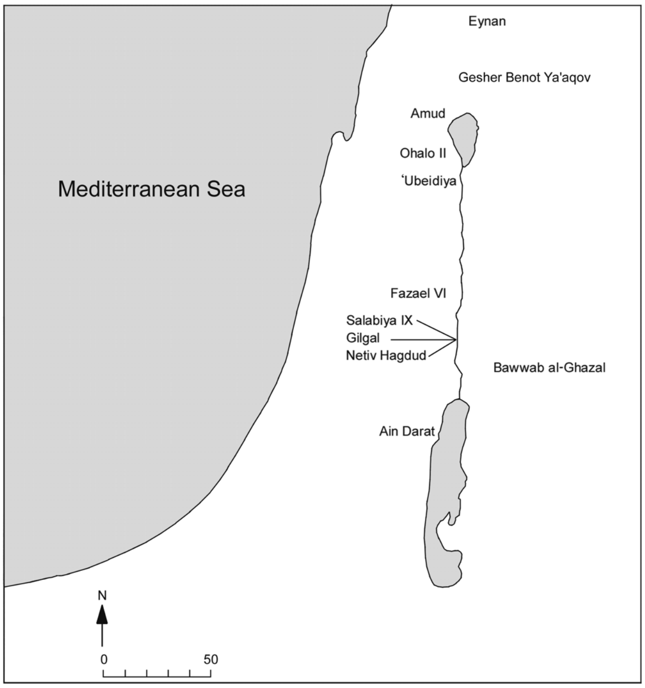

Figure 1. Location of Jordan Valley archaeological sites.

Table 1. Cultural periods of Jordan Valley archaeological sites.

Site	Date
ʻUbeidiya	Developed Oldowan
Gesher Benot Yaʻaqov	Acheulian
Amud	Middle Paleolithic
Ohalo II	Epipaleolithic
Eynan (Mallaha)	Natufian (combined)
Bawwab al-Ghazal	Natufian/Late PPNB
Netiv Hagdud	PPNA
Gilgal	PPNA
Ain Darat	PPNA
Fazael VI	PPNA
Salabiya IX	PPNA

Table 2. Jordan Valley archaeological sites indicating number of identified avian specimens (NISP) per site and number of identified avian taxa per site

Site	NISP	N Taxa	Source
ʻUbeidiya	724	42	Tchernov (1980)
Gesher Benot Yaʻaqov	63	16	unpublished data in the author's possession
Amud	6	6	unpublished data in the author's possession
Ohalo II	1350	83	Simmons & Nadel (1998); Simmons (2002); unpublished data in the author's possession
Eynan (Mallaha)	977	52	Pichon (1987); Valla et al. (n.d.)
Bawwab al-Ghazal	389	30	Kinzelman (2003)
Netiv Hagdud	1138	34	Tchernov (1994)
Gilgal	51	10	Noy et al. (1980)
Ain Darat	24	10	unpublished data in the author's possession
Fazael VI	31	21	unpublished data in the author's possession
Salabiya IX	72	23	unpublished data in the author's possession

Table 3. The avifauna of Amud Cave.

Family	Taxon	Element	Preferred Habitat
Anatidae	*Anas platyrhynchos*	right distal humerus	aquatic
Phasianidae	*Alectoris chukar*	right distal humerus	semi-arid, rocks
Scolopacidae	*Vanellus vanellus*	right proximal ulna	fields
	Scolopax rusticola	left proximal humerus	fields-scrub
Corvidae	*Corvus corone*	left distal tarsometatarsus	fields
	Corvus monedula	left distal tarsometatarsus	fields

well have captured them and brought them into the cave.

Data from each time period and each site will be discussed individually and synchronic analyses of both the Natufian sites and the PPNA sites will be offered here. A diachronic analysis of habitat, site seasonality, the development of sedentism, and changes in bird type and body part preference will also be presented.

Seasonality

Data concerning the distribution of individual bird taxa throughout the year was obtained from Paz & Eshbol (1992) and, as such, is based on the known month-by-month occurrence in Israel at the present time. Species classified as "Accidental" were not included in the analysis of the archaeological fauna, as current data on sightings of these birds consist of reports of single events, which do not lend themselves to inclusion. It should be noted, however, that none of the Accidental species present archaeologically are well represented (in terms of NISP) at any of these sites. In addition, extinct species from the sites of 'Ubeidiya and Gesher Benot Ya'aqov (GBY) have also been omitted from this analysis, as their seasonal presence in the Jordan Valley is unknown.

The figures representing the presence of avian taxa throughout the year were prepared for each site in the following manner. All taxa for each site were listed and the number of species per month commonly present, rarely present, absent, or nesting were counted. Thus, the graphs should be interpreted as depicting the potential for each bird taxon to be present during a particular month of the year, but they should not be seen as reflecting the frequency of a particular species on the site (e.g., NISP or MNI).

Figure 2 depicts the seasonal presence of birds at 'Ubeidiya and at GBY. Both sites exhibit the typical peak in numbers of species present during the winter months that still characterizes the Jordan Valley today, particularly around the Sea of Galilee, where many species winter or stop on the lake during their migration. It is notable that *all* of the bird taxa identified from the archaeological layers at GBY are likely to be found there from the month of November through the month of February; this is an unusual pattern for any site and is certainly evocative of a seasonal camp. At GBY, however, the skeletal element distribution patterns meet normal taphonomic expectations for a lakeshore, i.e., primarily dense elements such as coracoids are present. Furthermore, the bird bones of neither site exhibit cutmarks (admittedly rare on bird bones at any site), so there is nothing to indicate use of avifauna as a food source. These birds may thus represent the natural paleo-configuration of the bird population's constituents in winter. While intriguing, the winter peak cannot be attributed unequivocally to hominid predation or butchery activity at these sites.

While the seasonal distribution of birds at Ohalo II is not significantly different from that of the earlier sites, again exhibiting the typical winter peak (Figure 3), the interpretation of site seasonality based on these data does differ. The Epipaleolithic inhabitants of Ohalo II possessed both projectile (Nadel et al. 2002; Nadel 2002, 2003) and snare and net technology (Nadel et al. 1994; Nadel & Zaidner 2002) and probably were responsible for the accumulation of the bird remains within the huts and hearths on the site. In addition, some specimens also

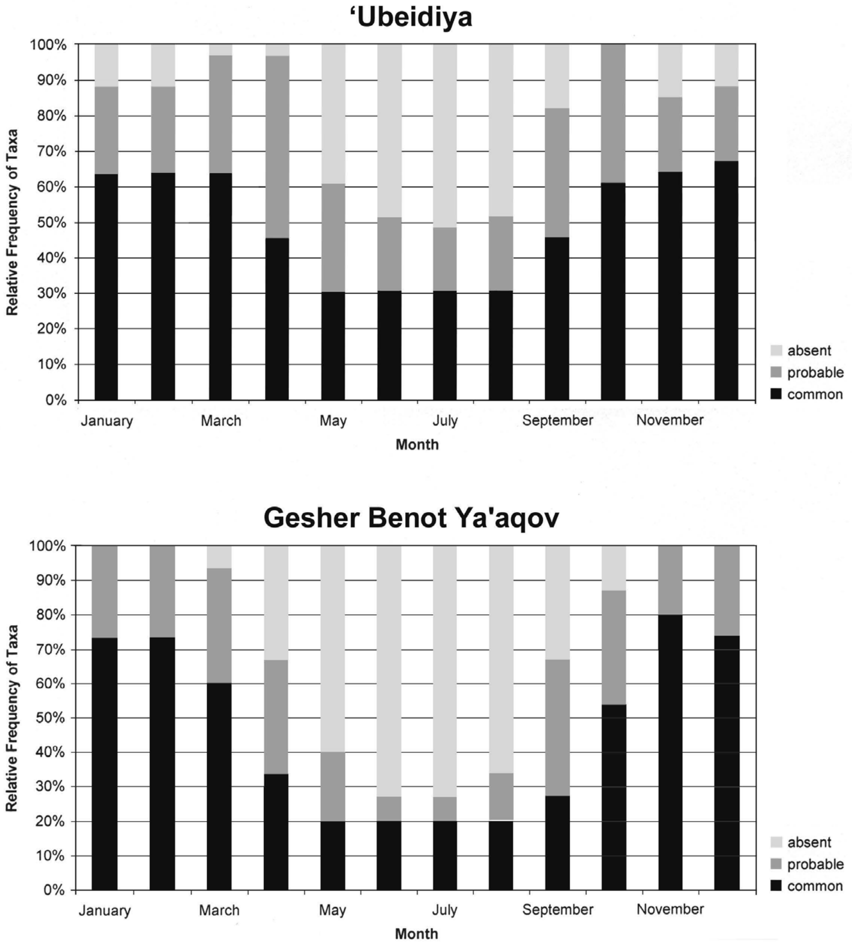

Figure 2. Seasonal presence of birds at ‘Ubeidiya and Gesher Benot Ya‘aqov.

exhibit cutmarks, both for meat removal and the stripping of flight feathers. Given the high frequency (60% of the total assemblage) of water and shore birds present at the site, it seems likely either that Ohalo II represents a series of seasonal encampments during the winter months or that (as suggested by Simmons & Nadel 1998; Nadel 2002) it was inhabited year-round, with birds being exploited most heavily during the months of their peak winter presence.

The seasonal distribution of birds at the Natufian site

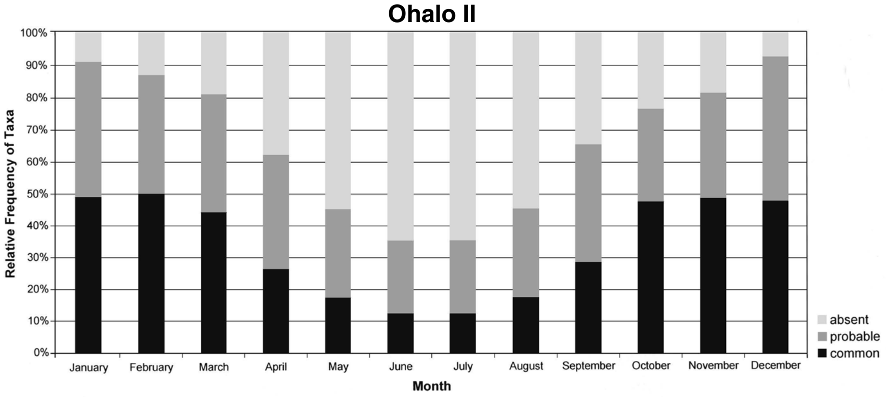

Figure 3. Seasonal presence of birds at Ohalo II.

of Eynan and Natufian levels at Bawwab al-Ghazal are presented in Figure 4. The Natufian assemblages maintain the pattern of a winter peak, with a somewhat precipitous drop in taxa present during the late spring and summer months. Both sites are situated near the shores of shallow lakes, which attracted large numbers of wintering and migratory waterfowl. Although the Natufian period is considered to reflect the beginnings of sedentism in the Levant, the avifauna does not provide convincing data in support of the exploitation of birds the year round. Rather, the graphs portray the continuing seasonal exploitation of waterfowl during the winter months as well as the taking of migratory species in the spring and autumn. Wintering species identified at both sites include high numbers of various ducks, as well as the coot (*Fulica atra*). These waterfowl possess a high fat:lean meat ratio and may have provided a much needed dietary resource for the winter months.

A definitive change in the seasonal distribution of avian taxa in Jordan Valley archaeological sites occurs with the advent of the PPNA. As seen in Figure 5, which depicts Netiv Hagdud as representative of the four PPNA sites examined, while a slight peak during the winter months persists, the species present during summer months attain nearly the same significance as wintering or migrating taxa. This is a significant indicator of two things. First, it indicates the importance that birds have achieved as a subsistence resource. The demands of pursuing horticulture intensively

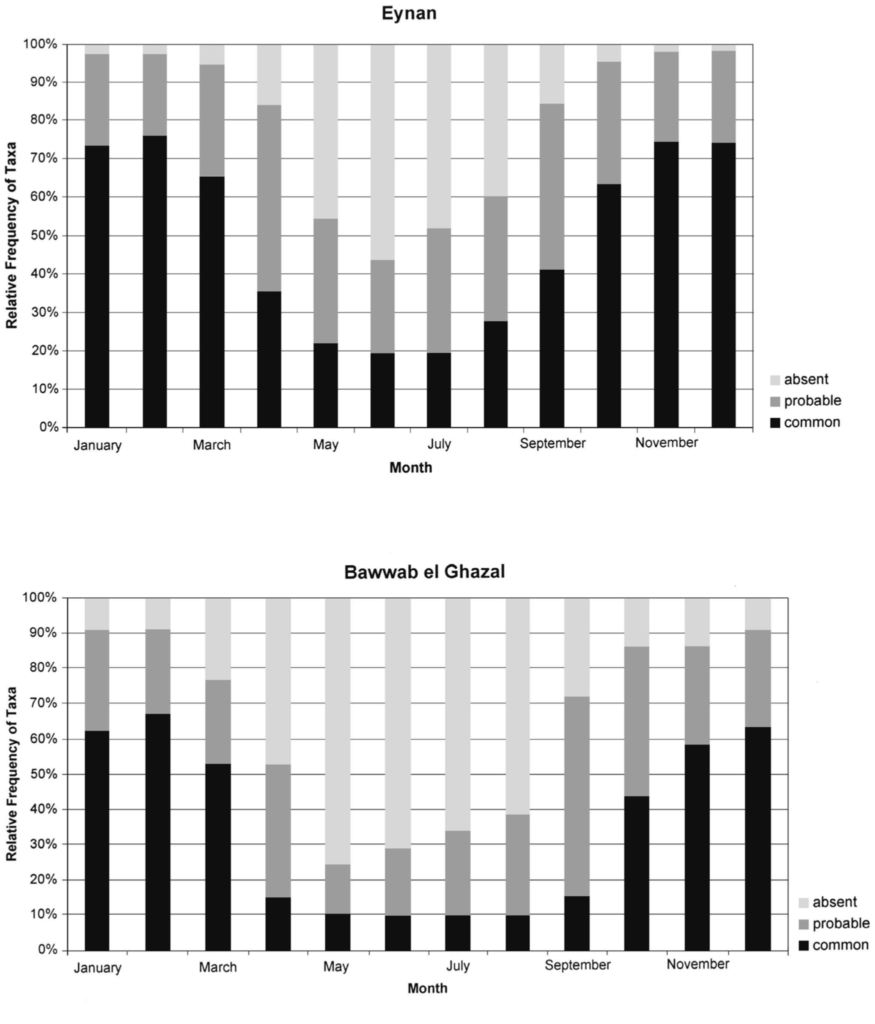

Figure 4. Seasonal presence of birds in the Natufian.

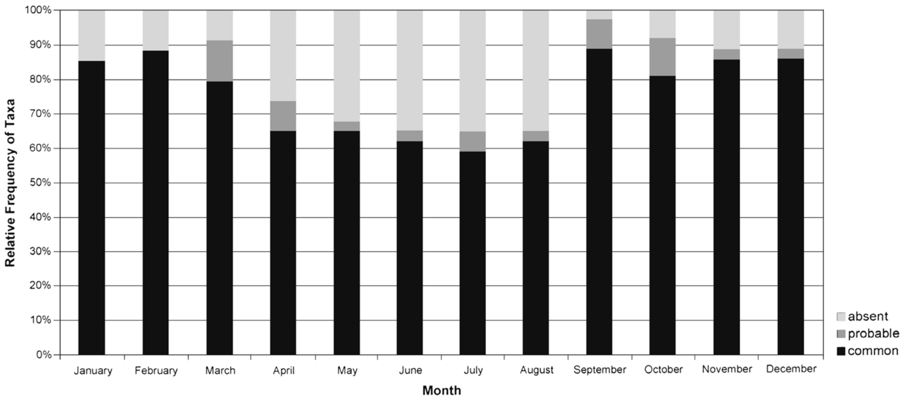

Figure 5. Representation of the seasonal presence of birds in the PPNA (Netiv Hagdud depicted here).

may have shifted the attention of PPNA peoples to smaller game. One may also argue that the increased predation on birds throughout the year may reflect the increase in the human populations during this time (e.g., Stiner et al. 1999). Second, Goring-Morris & Belfer-Cohen (1998) argue that populations were also contracting into smaller areas around stable bodies of water during the continuation of the climatic degradation of the Younger Dryas. Changes in the environment during this time period are clearly reflected in the human exploitation of birds (Pichon 1991; Tchernov 1993, 1994), particularly with the encroachment of the arid zone.

Figure 6 shows the relative frequency of bird species throughout the year from the Late Pre-Pottery Neolithic B (PPNB) levels at Bawwab al-Ghazal. Once again, a sharp difference occurs here, with a return to the earlier pattern of exploitation of waterfowl (primarily coots, cf. Kinzelman 2003) that wintered on a shallow lake the presence of which is inferred from botanical remains (R. Neef, personal communication, 1998). There is little evidence that the PPNB peoples of this site exploited birds throughout the year, as all species identified at Bawwab al-Ghazal can be found during the winter months from September through March. This is particularly interesting as the Late PPNB represents "a veritable population explosion" during a time of "climatic optimum and stability" (Goring-Morris & Belfer-Cohen 1998:85) when one might expect population pressure to demand exploitation of all resources to the utmost. However, as the excavators of Bawwab al-Ghazal have interpreted the site as a seasonal hunting camp supplying the community of Ain Ghazal (Wilke et al. 1997; Rollefson et al. 1999), the nature of this assemblage differs somewhat from those previously discussed.

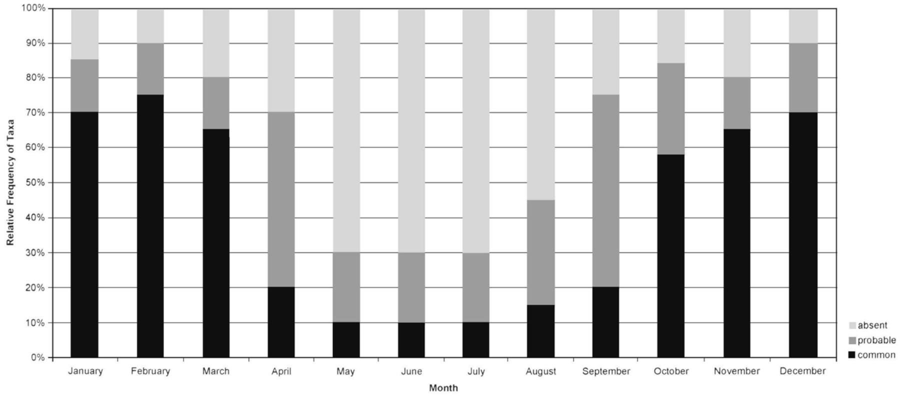

Figure 6. Seasonal presence of birds in the Late PPNB levels of Bawwab al-Ghazal.

Climate and environment

The habitat preference for each avian species provides information about the environment surrounding a site and about how people may have exploited each environmental zone and niche. Because some birds are specialists, having narrowly defined ecological niches and specific habitat preferences, these species are particularly useful for identifying the existence of a specific vegetation zone or micro-habitat. Other birds are generalists, using several different zones for different purposes, perhaps nesting on marshy islands, feeding in deeper waters, and raising their young in the tall grass at the lakeshore. When both types are present they provide a very accurate picture of the prevailing paleoenvironmental conditions at a site. Thus, by identifying birds to taxa, it is possible to pinpoint certain trends in the distribution of natural habitat surrounding archaeological sites and human exploitation of the environment over time. While aquatic habitats were clearly of the greatest importance to prehistoric peoples of all time periods, other habitats were also exploited to varying degrees.

Each of the figures representing the preferred habitat of avian taxa was prepared for each site in the following manner. All taxa for each site were listed and the preferred habitat noted, i.e., the habitat in which the bird may be most commonly seen. The total number of taxa preferring a particular habitat was tallied and the graphs represent the percentage of taxa preferring each habitat. Thus, the graphs must be interpreted with care. For sites such as 'Ubeidiya and GBY (all levels combined at both sites) where no evidence unambiguously suggests hominid predation of birds, these graphs (Figure 7) may more accurately depict the actual distribution of the environment surrounding the site. The site of 'Ubeidiya appears to have been surrounded by an amalgamation of many habitats, centered on the lake and its shore, but consisting largely of grasslands and woodlands, with some rocky areas. In contrast, GBY is represented by an overwhelming majority of aquatic and shore birds, with a small percentage of grassland species, most of which (primarily geese) also utilize the water.

The Epipaleolithic site of Ohalo II is also dominated by aquatic and shore taxa (combined they are 60% of all taxa), although there is compelling avifaunal evidence to suggest that the environment was drying and the vast grasslands seen in the Acheulian were fragmenting (Figure 8). While 22% of the taxa prefer grasslands, the rest (combined 18%), including those that are habitually found in rocky environs, arid zones, or scrub forest, are present in equal percentages. There is ample evidence in the form of both cutmarks and a preponderance of a single species (the great crested grebe, *Podiceps cristatus*) at Ohalo II to indicate the active hunting and consumption of birds (Simmons 2002). The distribution of preferred habitats

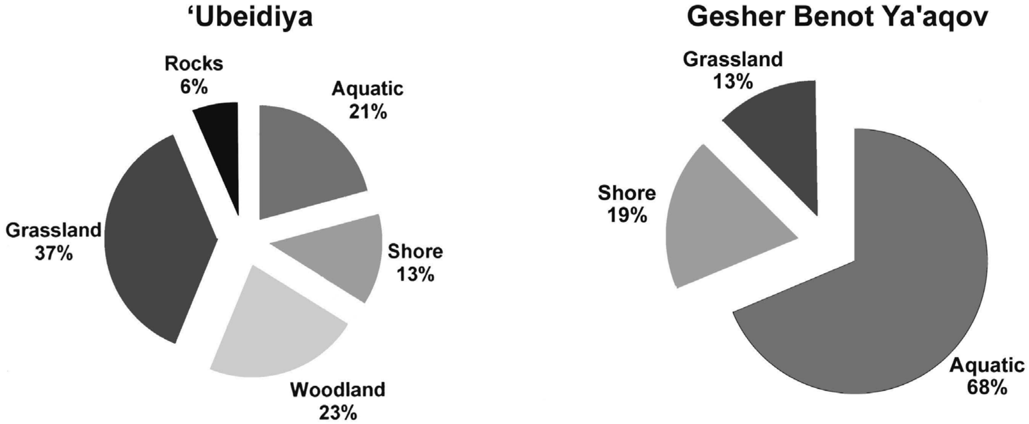

Figure 7. Preferred avian habitats at 'Ubeidiya and Gesher Benot Ya'aqov.

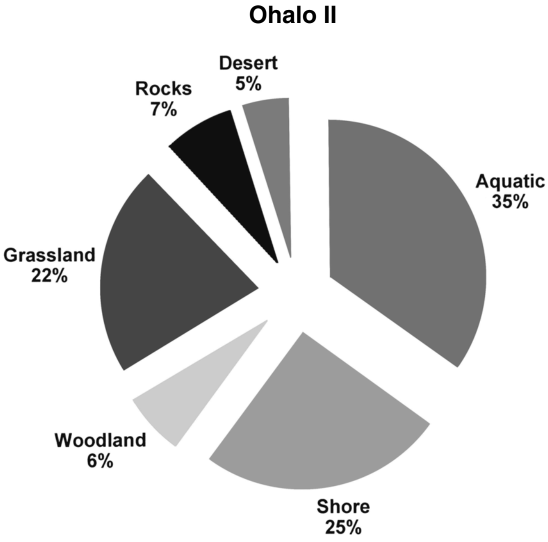

Figure 8. Preferred avian habitats at Ohalo II.

likely represents the pattern of environmental use by the Ohalo II peoples as well as the natural proportion of these habitat zones surrounding the site.

A marked change in the environment occurs in the Natufian, represented here by Eynan and Bawwab al-Ghazal (Figure 9). The sites are nearly uniform with regard to avian taxa, and hence exhibit similar distributions for habitat preferences. There are slight differences between the two sites, but the emphasis is overwhelmingly on aquatic species with those preferring the shore, grasslands and woodlands of considerably less importance. Much of the Natufian was very wet indeed, and taking advantage of large flocks of migrating and wintering waterfowl was apparently of critical importance to these peoples as a source of dietary fat. The exploitation of arid and rock dwelling birds at Eynan is the only notably distinguishing characteristic when comparing these sites.

Yet another critical transformation occurs with the PPNA sites (Figure 10), as the contraction of the population into well-defined centers during the climatic deterioration is reflected in the pattern of avian exploitation. All three sites depicted in Figure 10, Salabiya IX, Netiv Hagdud, and Gilgal, illustrate the fragmentation of the environment and the pressures of an expanding population in this depleted environment. The importance of aquatic species has dropped considerably, probably due to the shrinkage of the lakes in both size and depth during this time period. This is also borne out by the rise in the importance of arid species (the most important of which is the chukar, *Alectoris chukar*), which comprise some 9–12% of the taxa at these sites. Grassland and woodland species are important at all three sites, whereas birds preferring rocky habitats are also significant at both Netiv Hagdud and Gilgal. As all three sites are within visual distance of one another, it is interesting that the Salabiya peoples ignored birds of rocky areas; this is not an issue of sample size, as

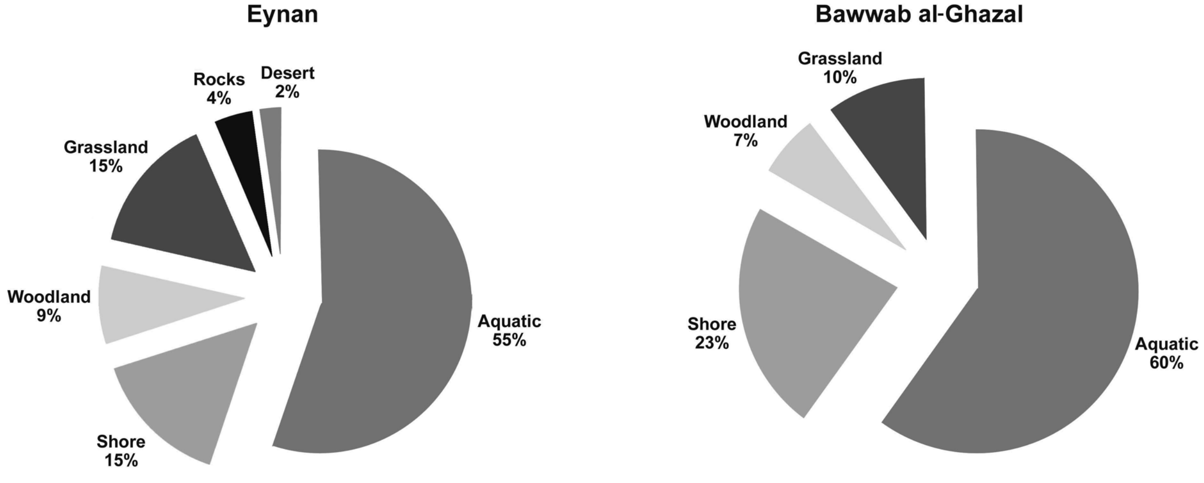

Figure 9. Preferred avian habitats in the Natufian.

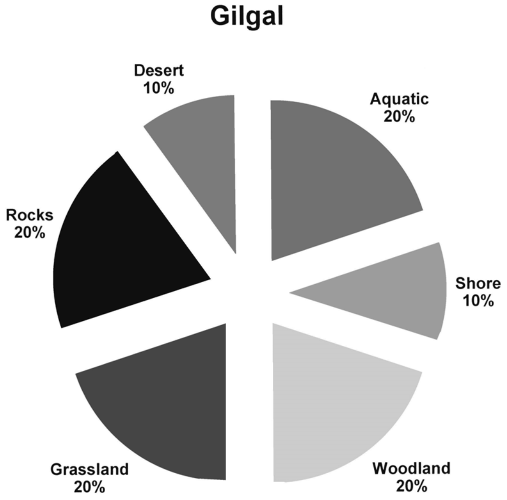

Figure 10. Preferred avian habitats in the PPNA.

with regard to both NISP and N Taxa (Table 1), Salabiya IX is better represented than Gilgal.

Overarching trends and singular quirks

Diachronically, several additional trends are notable in the data concerning the presence of and/or preference for certain avian Families and taxa (Figure 11). Three Families, the Anhigidae, the Podicipedidae and the Phalacrocoracidae, are all relatively primitive fish-eating birds, which are present only in the early part of the archaeological record. The Family Anhinga, represented by the darter (*Anhinga rufa*), is present at the earliest two archaeological sites, 'Ubeidiya and GBY. While it was a common winterer in Israel until the drying of Lake Hula in the 1950's, in the archaeological record of avifauna the darter vanishes from the Jordan Valley subsequent to the GBY sequence. Its presence at 'Ubeidiya is relatively incidental, comprising only 2% of the total avian assemblage at the entire site; however, it represents some 18% of the total avian assemblage at GBY and, most interestingly, is restricted to the older levels, including II-2, II-5, II-6, and II-7. The disappearance of *Anhinga rufa* at GBY by level V-5/6 may be indicative of a change in the water level of the lake adjacent to the site. The darter requires relatively deep water, more than 1–2 meters, in order to fish. There is no evidence that the darter was part of the hominid diet at either 'Ubeidiya or GBY (and no evidence that it was not). While one might argue that the darter would not be a preferred food for later peoples due

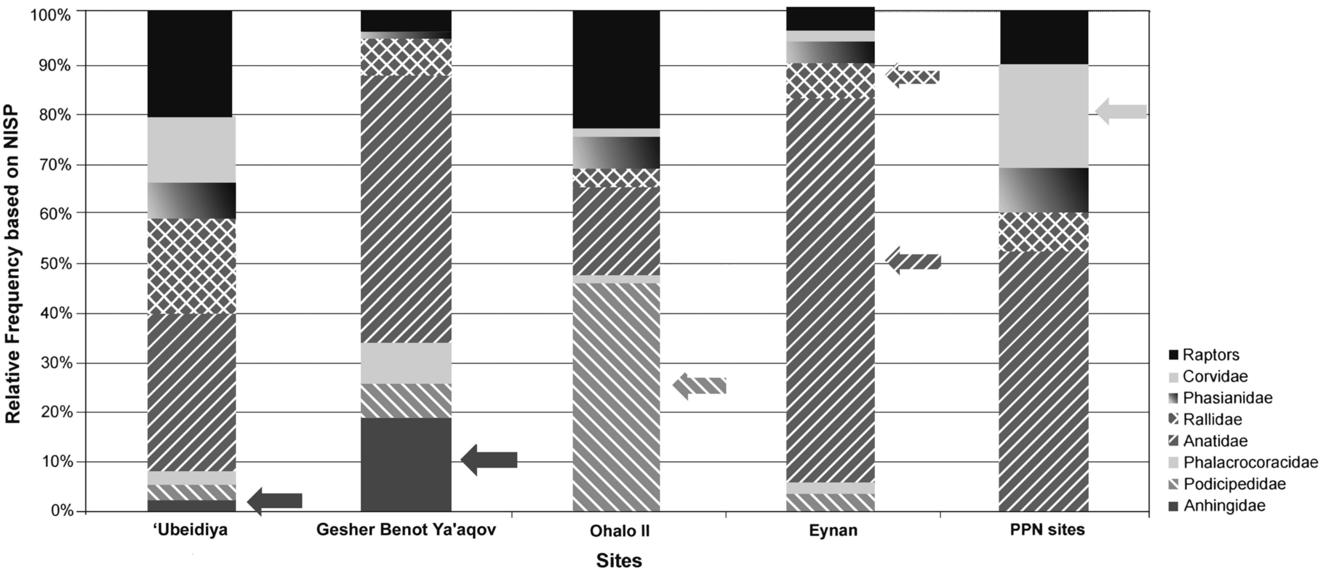

Figure 11. Relative frequencies of avian Families on archaeological sites over time.

to the fishy nature of its diet (and hence the taste of its own meat), later peoples at Ohalo II preferentially exploited the equally fishy-tasting great crested grebe (see below). The Family Phalacrocoracidae (cormorants) is also not well represented on most archaeological sites, and its last appearance is in the Natufian at Eynan.

The Family Anatidae assumes the greatest global importance at all sites in the Jordan Valley, although the degree of dependence on ducks, geese and swans varies through time (Figure 11). At ʻUbeidiya and GBY they represent some 33% and 55% of all taxa, respectively; again, there is no unequivocal evidence that this reflects the actions of hominids on the avifauna. At Ohalo II, species of Anatidae comprise only 18% of the total taxa, the third most important group behind the Podicipedidae (grebes) and the raptors (diurnal and nocturnal combined). Large numbers of bones in the "tri-osseum complex" (Tchernov 1994), the coracoid, sternum, and scapula, suggest that the breast meat of swans and geese (and presumably ducks as well, although no cutmarks have been identified on their bones) was an important dietary component for the Ohalo II peoples. However, at Ohalo II they were simply not as important as the grebes. It is not until the Natufian that one witnesses a marked increase in the numbers of the Anatidae in the archaeological record (Figure 11). At Eynan and also in the Natufian of Bawwab al-Ghazal, the species of the Family Anatidae comprise 78% and 65% of the avian taxa, respectively. At Eynan, in particular, this group overwhelms all other bird types. At Bawwab al-Ghazal, the coot, at some 33% of the total avian taxa, is also highly valued (Kinzelman 2003); the coot is significant at Eynan (Valla et al. n.d.), although not as dominant in this assemblage (Figure 11). While a few bones of geese and swans are present in these two Natufian assemblages, the ducks are the preeminent resource. At Eynan (Pichon 1984, 1987) it is the mallard (*Anas platyrhynchos*) and at Bawwab al-Ghazal (Kinzelman 2003) it is the teal (*Anas crecca*) that exhibit the highest NISP and MNI. The PPNA sites of Gilgal and Netiv Hagdud also exhibit a preference for Anatidae, which comprise 78% and 57% of their avian assemblages, respectively. The peoples of Netiv Hagdud (Tchernov 1994) also exploited birds of the Family Corvidae in large numbers, accounting for some 29% of the bones in the assemblage (Figure 11).

The Family Podicipedidae (grebes) is present in the earliest sites and persists through the Natufian (albeit in small numbers), where it subsequently disappears from the archaeological record. At the site of Ohalo II (Simmons & Nadel 1998; Simmons 2002), grebes account for some 45% of the NISP and are thus the single most important taxon at this Epipaleolithic site (Figure 11). At certain loci (the brush hut of Locus 13, in particular) bones of the great crested grebe (*Podiceps cristatus*) comprise 89% of the avian remains. Besides being used for food, *P. cristatus* may have been valued for its insulating breast feathers as well as the decorative feathers of its crest. The Ohalo II peoples probably captured grebes in large numbers by stringing nets across the channels in the marshy reeds near the lakeshore, a preferred habitat of the great crested grebe during its nesting season.

Raptors, both diurnal (the Families Accipitridae and Falconidae) and nocturnal (primarily the Family Strigidae), are ubiquitous on archaeological sites in every archaeological period (Figure 11). With only one exception, Netiv Hagdud, raptors were probably not considered a primary food resource. Tchernov (1994) reports that bones of the tri-osseum complex are prevalent for the black kite (*Milvus migrans*), thus indicating that these birds were consumed for their breast meat. At Ohalo II, the remains of *all* raptor species include numerous bones of the tri-osseum complex as well as other meat-bearing bones; it therefore seems likely that the Epipaleolithic people of this site also consumed raptors as a normal, albeit small, portion of their diet. Most of the evidence concerning the use of raptors on archaeological sites, however, dating from Ohalo II through the PPNA, suggests that these birds were valued for their talons and flight feathers. A series of hack marks on the tarsometatarsus of an eagle owl (*Bubo bubo*, the largest owl species in the Levant) from Eynan indicates the cutting of the tendons to the feet to ease the removal of talons (Valla et al. n.d.). Ulnae from Ohalo II raptors exhibit longitudinal striations resulting from the stripping of flight feathers. At all sites, pedal elements and wing elements (the latter in slightly lower percentages) dominate the raptor assemblages.

Beginning in the Epipaleolithic, the quail (*Coturnix coturnix*) was the most important game bird. The breast meat skeletal complex is always present in high proportions, as are the bones of the leg, primarily the tibiotarsus (Simmons 2002). Although *Alectoris chukar*, a larger bird of the Family Phasianidae, was also exploited, the chukar never superseded the quail as a food source, despite its presence on most sites. Its presence is, however, indicative of something important. The arrival of the chukar, or changes in its frequency, can often herald the encroachment of the desert zone. This can be viewed via percentages of other species preferring a more arid habitat as well (e.g., the steppe eagle, *Aquila rapax*), yet none is as frequent on archaeological sites as the chukar.

Thus, changes in the relative frequency of avian Families over time may provide information concerning: (1) the presence, absence, and relative frequency of those Families in the Jordan Valley; (2) the distribution of various vegetation belts and habitats, as well as changes in lake level; and (3) the preferences of prehistoric peoples for certain types of birds over time.

Discussion and conclusions

In sum, the avifaunal data from the Jordan Valley sites provides information concerning the following trends: (1) diachronic changes in the composition of the avian community from 1.4 million years ago through ca. 7,000 years ago; (2) changes in the usage of particular species of birds (e.g., Anatidae) and/or groups of birds (e.g., raptors) present in this part of the Rift Valley through time; (3) changes in the seasonal round and evidence for sedentism in human populations related to their exploitation of birds; and (4) shifts in vegetation zones and micro-habitats which may, at times, reflect changes in human population size and density.

Tchernov (1961, 1962) discussed the changing nature of the avifaunal community in the Levant and was particularly concerned with the shift from Ethiopian forms toward the end of the Miocene, which reflected a hot and humid climate, and the subsequent invasion of northern forms, reflecting the cooling and drying of the region. Although tropical elements of an avian community still persist in the Levant in isolated ecological niches, the prevailing avifauna became typically Palearctic at the close of the Miocene (Tchernov 1962). The review of avifaunal data from Tchernov's (1980) monograph on 'Ubeidiya, as well as the analysis of new data presented here from GBY, suggest that while the 'Ubeidiya birds may include several extinct species and represent different biogeographic origins (including those classified as Palearctic, European, Mediterranean, Holarctic, and Ethiopian), the GBY community represents a solely Palearctic and Holarctic fauna, typified by Anhinga, grebes, cormorants, and the Anatidae. The shift in the avifaunal community origin can be interpreted in two ways: (1) if hominids are responsible for the GBY assemblage, GBY was inhabited strictly during the winter months when these birds would have migrated south to the Lisan; or (2) if hominids were not responsible for the GBY bird assemblage, then an arctic avifaunal community was the norm throughout the year at this time in the northern Jordan Valley. The latter would indicate a climatic extreme for which there is no other supporting evidence. Given the discrete nature of the levels at GBY, the former is the more likely explanation. A single extinct species, a large, probably tree-dwelling pheasant-like bird in the genus *Tetrao*, represented solely by a tibiotarsus, is present at GBY.

By the Epipaleolithic, however, the distribution of birds in the Jordan Valley resembles that of the present (Simmons & Nadel 1998), with perhaps a single exception, an extinct pheasant species from Locus 15 of Ohalo II (Nadel 2003). Certainly by the Natufian, all birds recovered archaeologically are in the same taxa as those present today (Pichon 1984, 1987; Tchernov 1993). By the Epipaleolithic (and perhaps earlier), the occurrence of bird taxa on archaeological sites becomes indicative of how the choices of prehistoric peoples actively affected their exploitation of the environment, rather than simply reflecting the natural distribution of birds within the environment surrounding the site. All areas of the environment were exploited, with most emphasis on aquatic and shore/riverbank areas. During the Epipaleolithic, semi-arid species assume some importance in the subsistence economy, though they comprise only 5% of the assemblage. The existence of an arid-zone avifauna may also reflect the gradual disappearance of the Lisan at this time and the movement of the desert belt into the upper Jordan Valley.

For the first time during the Epipaleolithic, birds of prey also assume significance, and both diurnal and nocturnal raptors are taken for their flight feathers and talons, primarily for decorative use. Although raptors were consumed at the site of Ohalo II (Simmons & Nadel 1998; Simmons 2002), for the most part raptor hunting signifies symbolism rather than subsistence. In more recent times, the use of any raptor species, specifically the black kite (*Milvus migrans*), for subsistence is reported only for the site of Netiv Hagdud (Tchernov 1993, 1994). The exploitation of birds of prey continues, however, for adornment and symbolic purposes throughout the Natufian and Pre-Pottery Neolithic (Pichon 1987; Tchernov 1994).

By the Natufian, people are making overwhelming use of aquatic species as a food resource and water birds comprise well over 50% of the avian niches exploited. The environment is wetter, with relatively few taxa preferring arid and semi-arid habitats found. At this time, open fields become an important source of game birds, with the emphasis placed on both the quail, beginning in the Epipaleolithic (Simmons 2002), and the chukar (Pichon 1984, 1987, 1989; Tchernov 1993), beginning in the Natufian.

The PPNA brings about another transformation, both in the landscape and in human paleoecology. As the lakes recede and desiccate, human use of the environment becomes less focused on aquatic habitats; the use of the environment fragments, with all habitat zones receiving equal exploitative emphasis. Semi-arid taxa comprise around 10% of the birds, bearing witness to the encroachment of the arid zone as well as the probable over-exploitation of certain areas and a concomitant depletion of local resources. Tchernov (1993:124) has alluded that a “centripetal ecological gradient will be created by the intensive anthropogenic activities” around a site. As Stiner et al. (1999) have also suggested, increased reliance on small prey correlates with human population expansion:

> The peripheral belts round the core of the site will show a gradual relaxation in the exploitation of the resources, but the width of these ecological belts will fluctuate due to the seasonal changes brought about in the carrying capacity of the area. Habitats will gradually turn to be more natural in the outer belts, so that hunting can be practiced only at a certain distance form the site. It is important to emphasize that the constant degradation of biological resources from and around early human settlements created a unique and isolated mini-ecosystem that was virtually devoid of most plants and animals, but opened new niches and opportunities for preadapted colonizers (Tchernov 1994:124).

Contrary to Tchernov’s (1993:129) suggestion that there is “an almost revolutionary broadening of the exploited animal species” during the Natufian, there is virtually no change in the diversity index (N Taxa/NISP x 100) for avian species from the earliest Jordan Valley site at ‘Ubeidiya (5.8) through Ohalo II (6.1) to Eynan (5.3); if anything, the diversity of species exploited actually drops in the PPNA, as seen at Netiv Hagdud (3.0). This assumes that all the archaeological bird assemblages discussed in this paper are anthropogenic. That larger numbers of birds (and other small game) relative to ungulates, etc. do occur beginning in the Natufian is undisputed (Tchernov 1991, 1993; Stiner et al. 1999). Nevertheless, the apparent increase in avian species diversity seen with the advent of sedentism is probably an artifact of sample size: the smaller the NISP, the fewer taxa identified, and this is true of all sites regardless of age.

The avifaunal evidence from Jordan Valley sites supports much of what has already been documented via other faunal and geological data regarding the shifting of vegetation zones and habitats, the human population expansion with concomitant contraction into smaller areas, as well as the gradual climatic shifts in the region. The avifauna indicates that 'Ubeidiya (averaged for all strata) was drier than GBY, and that the environment was drying in the Epipaleolithic, wetter in the Natufian, and drier still in the Pre-Pottery Neolithic. Data from birds also provide additional information regarding variations in habitats exploited by people, their subsistence choices, their preferences for specific taxa, and how these species were utilized through time. Because birds are relatively specific in their ecological requirements, when sample size is sufficient to permit classification of preferred avian habitats a clearer picture of the micro-environmental zones surrounding an archaeological site may be rendered.

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References

Belmaker, M., Tchernov, E., Condemi, S. & Bar-Yosef , O. (2002). New evidence for hominid presence in the Lower Pleistocene of the southern Levant. *Journal of Human Evolution* **43**, 43–56.

Goren-Inbar, N., Feibel, C. S., Verosub, K. L., Melamed, Y., Kislev, M. E., Tchernov, E. & Saragusti, I. (2000). Pleistocene milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. *Science* **289**, 944–974.

Goring-Morris, N. & Belfer-Cohen, A. (1998). The articulation of cultural processes and late Quaternary environmental changes in Cisjordan. *Paléorient* **23**, 71–93.

Kinzelman, E. (2003). *The Avifauna of Bawwab al-Ghazal: A Zooarchaeological Analysis*. Unpublished Master's Thesis, Department of Anthropology, Western Michigan University, Kalamazoo.

Nadel, D. (2002). Indoor/outdoor flint knapping and minute debitage remains: the evidence from the Ohalo II submerged camp (19.5 ky, Jordan Valley). *Lithic Technology* **26**, 118–137.

Nadel, D. (2003). The Ohalo II flint assemblage and the beginning of the Epipalaeolithic in the Jordan Valley. In (N. Goring-Morris & A. Belfer-Cohen, Eds.) *More than Meets the Eye: Studies on Upper Palaeolithic Diversity in the Near East*. Oxford: Oxbow Books, pp. 216–229.

Nadel, D., Danin, A., Werker, E., Schick, T., Kislev, M. & Stewart, K. (1994). 19,000-year-old twisted fibers from Ohalo II. *Current Anthropology* **35**, 451–458.

Nadel, D., Gharaieb, T. & Halabi, H. (2002). The flint assemblage. In (D. Nadel, Ed.) *Ohalo II: A 23,000-Year-Old Fisher-Hunter-Gatherers' Camp on the Shore of the Sea of Galilee*. Catalogue 20. Haifa: Reuben and Edith Hecht Museum, pp. 42–48.

Nadel, D. & Zaidner, Y. (2002). Upper Pleistocene and mid-Holocene net sinkers from the Sea of Galilee, Israel. *Mitkufat Ha'even, Journal of the Israel Prehistoric Society* **32**, 49–72.

Noy, T., Schuldenrein, J. & Tchernov, E. (1980). Gilgal, a Pre-Pottery Neolithic A site in the lower Jordan Valley. *Israel Exploration Journal* **30**, 63–82.

Paz, U. (1987). *The Birds of Israel*. Worcester: Billing and Sons (English translation by Christopher Helm).

Paz, U. & Eshbol, Y. (1992). *Photographic Guide to the Birds of Israel According to Habitat*. Jerusalem: Keter Publishing House (in Hebrew).

Pichon, J. (1984). *L'Avifaune Natoufienne du Levant*. 2 tomes. Thèse de 3è cycle, Université Pierre et Marie-Curie, Paris VI, Paris.

Pichon, J. (1987). L'Avifaune. In (J. Bouchud, Ed.) *La Faune du Gisement Natoufien de Mallaha (Eynan), Israel*. Mémoires et Travaux de Centre de Recherche Français de Jérusalem 4. Paris: Association Paléorient, pp. 115–150.

Pichon, J. (1989). L'Environnement du Natufien en Israel. In (O. Bar-Yosef & B. Vandermeersch, Eds.) *Investigations in South Levantine Prehistory.* BAR International Series 497. Oxford: British Archaeological Reports, pp. 61–74.

Pichon, J. (1991). Les oiseaux au Natoufien, avifaune et sédentairité. In (O. Bar-Yosef & F. R. Valla, Eds.) T*he Natufian Culture in the Levant*. Archaeological Series 1. Ann Arbor: International Monographs in Prehistory, pp. 371–380.

Rollefson, G. O., Quintero, L. A. & Wilke, P. J. (1999). Bawwab al-Ghazal: a preliminary report of the 1998 testing season. *Neo-Lithics* **1/99**, 2–4.

Simmons, T. (2002). The birds of Ohalo II. In (D. Nadel, Ed.) *Ohalo II: A 23,000-Year-Old Fisher-Hunter-Gatherers' Camp on the Shore of the Sea of Galilee*). Catalogue 20. Haifa: Reuben and Edith Hecht Museum, pp. 32–36.

Simmons, T. & Nadel, D. (1998). The avifauna of the early Epipalaeolithic site of Ohalo II (19,400 BP), Israel: Species diversity, habitat and seasonality. *International Journal of Osteoarchaeology* **8**, 79–96.

Stiner, M., Munro, N., Surovell, T., Tchernov, E. & Bar-Yosef, O. (1999). Paleolithic population growth pulses evidenced by small animal exploitation. *Science* **283**, 190–194.

Tchernov, E. (1961). Outlines to the Paleolithic avifauna in Palestine. *Bulletin of the Research Council of Israel* **9B**(4).

Tchernov, E. (1962). Paleolithic avifauna in Palestine. *Bulletin of the Research Council of Israel* **11**, 95–131.

Tchernov, E. (1980). *The Pleistocene Birds of 'Ubeidiya, Jordan Valley*. Jerusalem: Israel Academy of Sciences and Humanities.

Tchernov, E. (1987). The age of the 'Ubeidiya formation, an early hominid site in the Jordan Valley. *Israel Journal of Earth Sciences* **36**, 3–36.

Tchernov, E. (1991). Of mice and men – Biological markers for human sedentism in the Middle East: A report. *Paléorient* **17**, 153–160.

Tchernov, E. (1993). Exploitation of birds during the Natufian and early Neolithic of the southern Levant. *Archaeofauna* **2**, 121–143.

Tchernov, E. (1994). *An Early Neolithic Village in the Jordan Valley, Part II: The Fauna of Netiv Hagdud*. American School of Prehistoric Research, Bulletin 44. Cambridge, MA: Harvard University, Peabody Museum of Archaeology and Ethnology.

Valla, F. R., Khalaily, H., Valladas, H., Samuelian, N., March, R., Bocquentin, F., Bridault, A., Rabinovich, R., Simmons, T., Le Dosseur, G., Bar-Yosef-Mayer, D., Miller-Rosen, A., Dubreuil, L. & Belfer-Cohen, A. (n.d.). Les fouilles à Mallaha en 2000 et 2001: 3ème rapport préliminaire. *Mitkufat Ha'even, Journal of the Israel Prehistoric Society* (in preparation).

Wilke, P. J., Quintero, L. A. & Rollefson, G. O. (1997). Bawwab al-Ghazal: Temporary station of hunting pastoralists in the eastern Jordanian desert. *Neo-Lithics* **3/97**, 12–13.

Chapter XIV

Natufian Behavior in the Hula Basin: The Question of Territoriality

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Abstract

It is felt that in humans the problem of territory (the relation of a living organism with its environment) is deeply embedded in a historical process, namely culture. On this basis, one can attempt to get insights into Natufian territoriality through three different approaches. I first try to trace limits and boundaries of possible Natufian territories through the provenience of objects imported to sites. I then look for the way territories were exploited by Natufian villagers as reflected by faunal analysis. Finally, I look for information about a possible sense of ownership among Natufian people as expressed through their behavior in relation to objects (e.g., decorative items and basalt tools), as well as animal domestication and settlement. As is often the case in prehistory, the results are not unequivocal. Nevertheless, none of these approaches really sustains the hypothesis that Natufian people would have defended a certain space against intruders. There are some hints that people were able to travel relatively long distances, overexploitation of resources seems improbable, and though a sense of ownership cannot be totally ruled out, its manifestations seem difficult to trace. These findings encourage me to question the validity of models of the origins of agriculture that are based mainly on climate changes and population pressure, that is on simple regulation of human populations by carrying capacity. I advocate the need for a broader theoretical framework and for more interest devoted to detailed cultural investigations.

Introduction

In this paper I would like to address the question of Natufian territories. But before entering the matter, a few preliminary notes should be made. Ecologists traditionally distinguish between "home range" and "territory." The home range is the area that individuals or groups traverse in their everyday life. Conversely, a territory is an area defended for exclusive use (Krohne 2001: 200). Oversimplified as they possibly are when applied to humans, these concepts should warn us about the wide range of behaviors we are dealing with when considering the relation of living bodies to the space in which they are moving.

Indeed, humans have a unique relation to their environment. This uniqueness is expressed in more than one way and bears direct consequences for our ability to reconstruct the environment that prehistoric people encountered thousands of years ago, the way they used it, and the way they understood it.

In this respect, one of the characteristics of humans is the ability to shape the landscape on a larger scale than any other species. This ability increased drastically with time. While this capacity is generally acknowledged for recent periods, at least from the Neolithic onward, it is usually minimized for earlier epochs. In fact, man's impact on his environment, not only the landscape, certainly started very early. There are many suggestions that this impact already had important effects by Natufian times (12,500–10,000 cal BC). Recognizing these effects will be one of our problems when dealing with Natufian territories. But we cannot ignore the later, broader, impacts of man on his environment, since these more recent changes were so drastic that they affected every aspect of the environment. The result is a deep shadow that makes any attempt at reconstructing the environment encountered by Natufian people an extremely difficult task.

In the Hula area, the focus of this study, we know of two changes that have drastically modified the ecological system since Natufian times. One was the introduction of agriculture, about 7,000 years cal BC, when people settled at Beisamoun (Lechevallier 1978), which was followed by thousands of years of farming activities. According to the findings of Tchernov & Horvitz (1990), this led to gradual destruction of natural habitats and lowering of carrying capacity, as evidenced by the replacement of cattle by caprovines (until the introduction of water buffaloes by the 8th century AD). The other change took place fifty years ago, when the villagers living in the area had to move and an industrial mode of exploitation was introduced that led to the drying out of the ancient lake and the pumping of the spring of Eynan (Dimentman et al. 1992).

Culture mediates and directs the ways humans interact with and shape their environment. This process has been at work at least since the origin of language. No society can survive without it. Culture organizes the relations of people with each other inside their own group and outside. Culture also gives meaning to the environment. It organizes a mental representation of the world so that it makes some sense to people. Moreover, culture provides rules to regulate the relations between society, its members, and the world they are part of. The more socialized an action, the more deeply it is embedded in culture. In the case I am concerned with here, ideas of territories, sedentism, and hunting habits will be controlled largely by culture, that is, by rules that are dependent on sophisticated traditions, not simple responses to external stimuli. But culture is a process. Concepts change through time, as do the behaviors they control. We cannot assume that ideas and behaviors we observe today in supposedly undisturbed hunter-gatherer societies have not changed over the last twelve thousand years. If people have retained a hunting and gathering economy, can we assume that there has been no change in culture? The teachings of prehistory strongly oppose this view. One of the main difficulties we have to face when trying to get some insight into Natufian territories will be to determine the meaning of this concept for people in this particular culture.

Finally, it should be noted that these activities of humans – shaping their environment, creating their own mental space – result in a reality that is superimposed on the physical world. In the early twentieth century some geographers became aware of this phenomenon and started to study it under the name "Human Geography." They devoted their attention to the analysis of the historical processes by which people had inserted themselves in a given landscape and had modified it to their own advantage. These processes started long ago, much earlier than the first protagonists of human geography could have thought. In a way, the concept of the "Levantine Corridor" as coined by Ofer Bar-Yosef (1989; see also Bar-Yosef & Belfer-Cohen 1992:38 and their Figure 6) is a good example of a concept that may have little grounding in pure physical geography but is amply justified in the field of human geography. It refers to those areas at the margin of the western desert of the Near East where societies ready to adopt a way of life based on food production evolved.

With this background in mind, I would like to investigate briefly what we know about the Natufian territory at Eynan. I assume that these people were living in a certain space that we call "territory." Since archaeologists generally consider them to be at least relatively sedentary people, we can assume as well that this territory extended around the village near the spring of Eynan. Now come the difficult questions. How are we to recognize this territory outside of the village itself? How are we to reconstruct the way this territory was used by people? What were the effects of this use on the resources they exploited? How did people understand their relation to the piece of land they lived on (and from)? How did they relate this piece of land to pieces of land used by nearby groups?

Territorial extension

It is very hard to reconstruct with any degree of accuracy the extent of the land exploited around any given Natufian site. One possible approach would be to plot the known sites on a map, establish the mean distance between them in a given area, and draw tentative conclusions from these results, in conjunction with considerations of the landscape and potential resources. This approach has proved successful in analyzing later-period settlement patterns. Unfortunately, it cannot work for the Natufian for at least two reasons: the probable disappearance of many sites and our poor chronological control of those we do know, preventing us from being able to establish the degree of contemporaneity among any of them.

A more reliable approach has been attempted during the past ten years. This approach involves tracing the origin of mineral and animal resources, particularly marine shells, found at the sites. When the sources can be located with accuracy, they can provide some idea about the "catchment area" of the people living there. The materials that can be traced using this approach have yielded results of three different kinds. Some materials came mainly from the vicinity of the site; this is the case for flint and ochre. Others came mainly from close to intermediate distances (let us say, as a broad estimation, 10–60 km); these are most decorative shells and basalt tools. The third category is provided mainly by obsidian, but some shells as well, which came from hundreds of kilometers away.

The meanings of these findings in terms of territory are not easily recognized. Flint and ochre seem to exemplify direct exploitation of the nearby environment. The area within which these materials were acquired may reflect the territory regularly used by the group (Delage 2001). Unfortunately, this hypothesis remains difficult to substantiate. The long-distance transport of obsidian from Cappadocia and marine shells from the Red Sea can be taken as evidence for group-to-group or down-the-line exchange. It is nevertheless interesting to note that each kind of material has a different pattern of distribution. Red Sea shells are common in the Negev and become rare north of it, where they are found as isolated items at several sites throughout the entire Natufian sequence (Mienis 1887; Reese 1991). In contrast, Cappadocian obsidian, which comes from outside the range of the Natufian culture, is known in the Middle Euphrates Valley only from the Late Natufian onward, and does not occur farther south except for Eynan, during the Final Natufian, when small quantities appear consistently (Cauvin 1991; Moore 1991; Khalaily in Valla et al. 2001). There is, then, at the current stage of knowledge, a kind of opposition between the observed distribution of Red Sea shells, with a relatively diffused pattern of isolated finds, and that of obsidian, which is concentrated in a small number of places. This may well mean that the two items were not transmitted in the same way.

More difficult to understand from the point of view of territory are the items that traveled intermediate distances from their source, like Mediterranean shells and basalt tools. Mediterranean dentalium shells can be found in relatively large quantities at Eynan, some 45 km away from the seashore. One can certainly imagine people going and collecting the shells themselves. They might also have acquired the shells through exchange. These hypotheses are not mutually exclusive.

Basalt tools add another dimension to the problem, for two reasons. First, they may be heavy and not easy to transport; second, they are not simply collected on the spot but are the result of lengthy work. Their distribution indicates that the farther the source from the site, the more limestone was used instead of basalt for the same purposes. It is also apparent that the average weight of transported items tends to diminish with distance (compare, for example, the inventories at Hayonim Cave and Wadi Hammeh 27 in Belfer-Cohen 1988:179ff; and Edwards 1991:133 and 136; the relative position of sites and sources is shown in Figure 1). These observations are not surprising. More intriguing are the results of the analyses of the sources of basalt at the three sites of Hayonim Cave, el-Wad, and Eynan. These results show that the tools at each site did not necessarily come from the nearest flow and that they may have come from more than one flow (Weinstein-Evron et al. 2001; see Figure 1). Taken together, the data underline the general

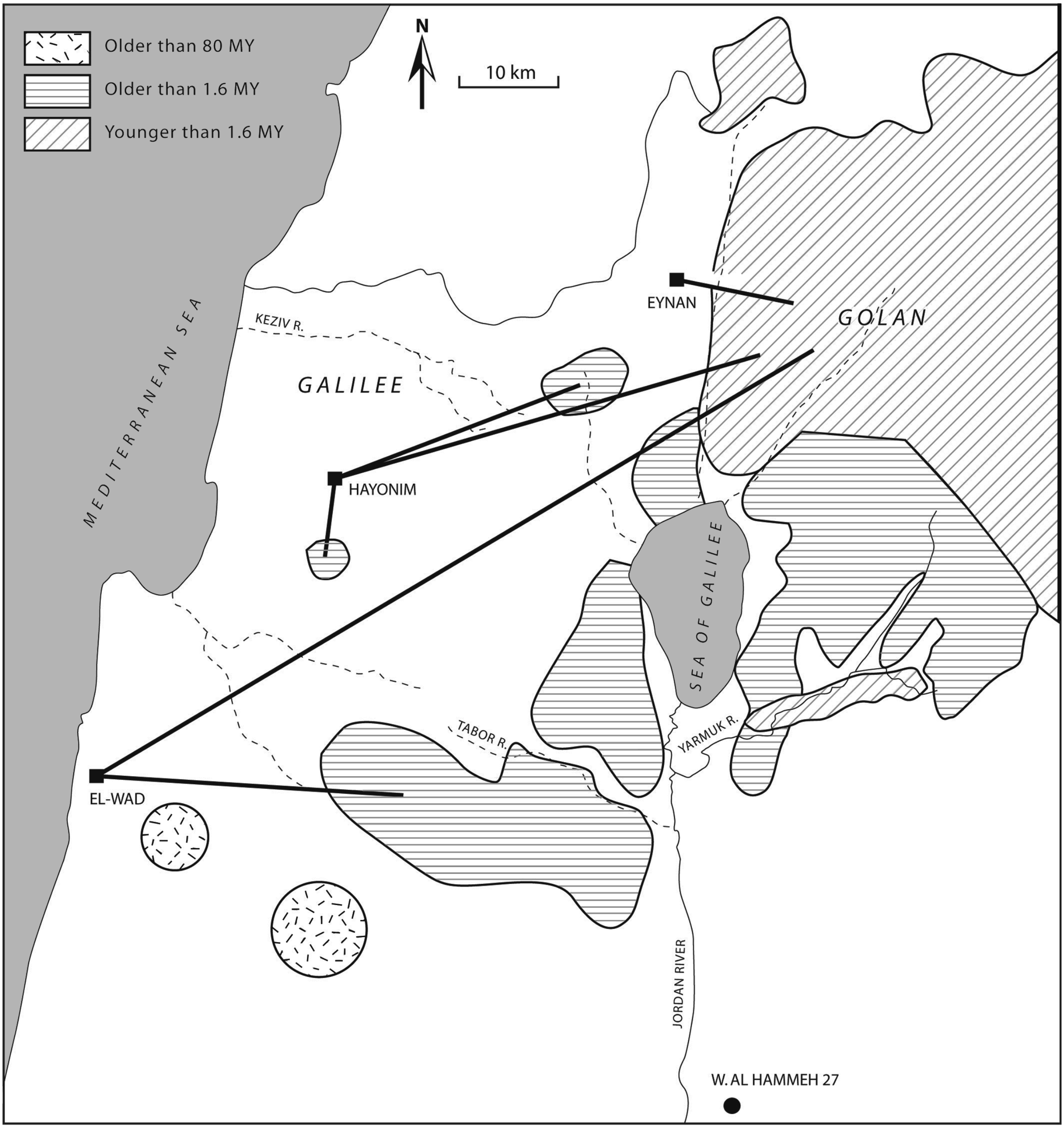
Older than 80 MY
Older than 1.6 MY
Younger than 1.6 MY
N
10 km
MEDITERRANEAN SEA
KEZIV R.
GALILEE
EYNAN
GOLAN
HAYONIM
SEA OF GALILEE
TABOR R.
YARMUK R.
EL-WAD
JORDAN RIVER
W. AL HAMMEH 27

Figure 1. Basalt sources used for tools at Hayonim Cave, el-Wad, and Eynan (after Weinstein-Evron et al. 2001).

tendency to live on local resources and again the possibility of trips toward desirable sources of raw material or exchange with other groups. As emphasized by Weinstein-Evron et al. (2001), the probability of exchange rises when dealing with basalt due to the work involved in the manufacture of these tools. But another option is possible:

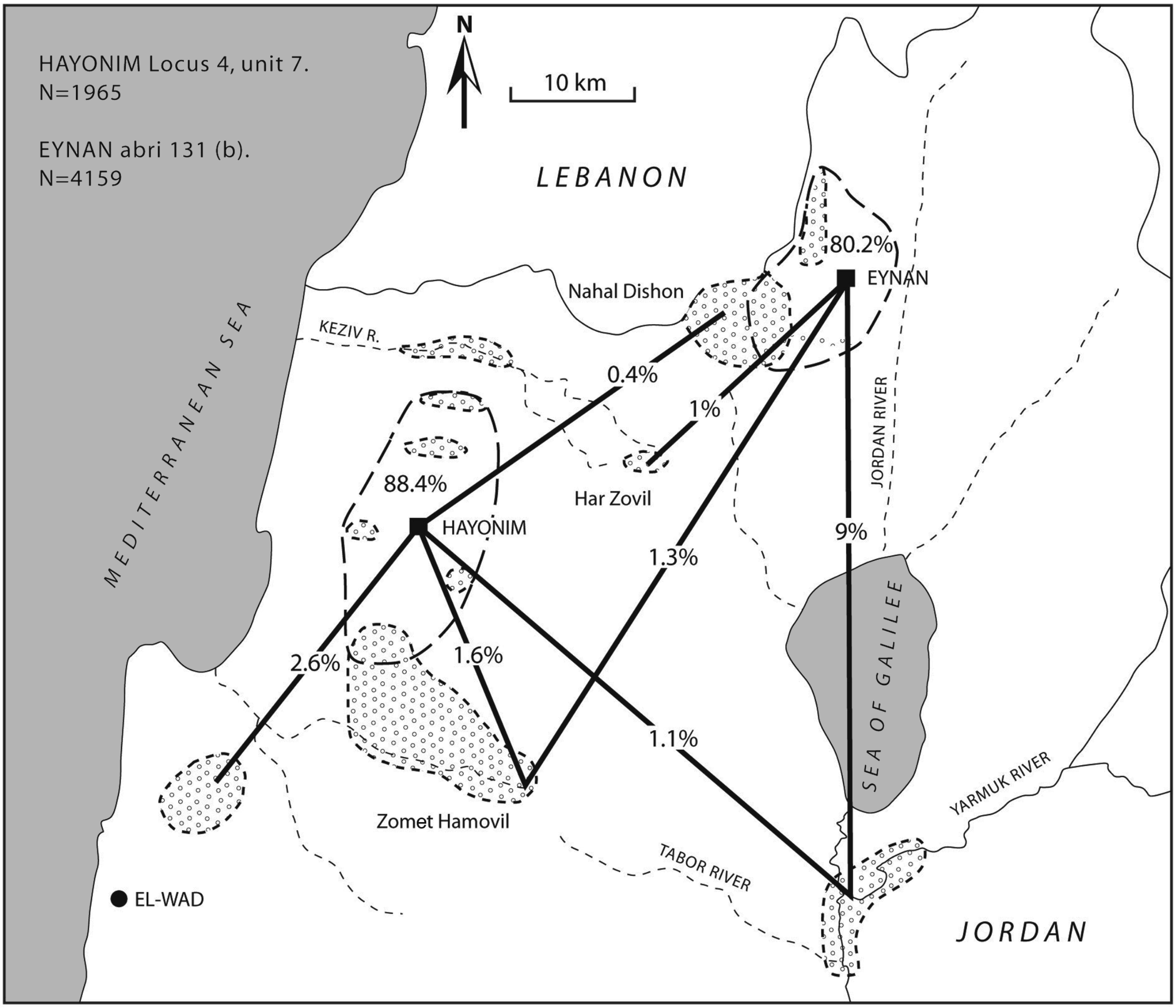
HAYONIM Locus 4, unit 7.
N=1965
EYNAN abri 131 (b).
N=4159
N
10 km
LEBANON
MEDITERRANEAN SEA
KEZIV R.
Nahal Dishon
80.2%
EYNAN
0.4%
1%
88.4%
Har Zovil
HAYONIM
1.3%
9%
JORDAN RIVER
SEA OF GALILEE
2.6%
1.6%
1.1%
Zomet Hamovil
YARMUK RIVER
TABOR RIVER
EL-WAD
JORDAN

Figure 2. Flint sources used by Early Natufian people from Hayonim Cave and Eynan (after Delage 2001).

people could have brought back the raw material with them in order to work it at home after quick pre-shaping on the spot. That may well have happened at least at sites relatively close to the sources.

All in all, what emerges from this brief review is that we are unable to get a clear idea of the extent of the territory around any given site. We can only be sure, from the facts that the flints were brought to the sites in large quantities, that people regularly utilized relatively small areas, some 20–25 km in diameter, around villages. There are hints that people were able to travel longer distances. Delage (2001) has found that inhabitants from Hayonim and Eynan probably visited the same sources, sometimes as far as about 40 km from each site. He also has noted that people from Hayonim possibly visited sources not far from Eynan and el-Wad (Figure 2). These findings suggest that people from Hayonim, but from other places as well, were able to move into territories much larger than the limited areas around each site (provided that the foreign flints were not brought in by visitors), and that they were able to share resources sometimes even relatively close to another group's settlement (provided, of course, that the sites in question were contemporaneously occupied).

Land use

If we have no means of clearly seeing the limits of any given territory around a Natufian village, nor of determining the area that a given group was able to use freely, is it possible to get some insight into the way groups took advantage of their territory? In this matter the excavated faunas are our main source of information. Eitan Tchernov has recently argued that the impact of Natufian villages on local environments was sufficient to create new habitats where human commensals could evolve within the villages themselves and around them. But besides this side effect, how was the territory exploited? Two aspects have often been emphasized. One is a suggested "cultural filter," according to which people preferentially hunted gazelles (Henry 1975; Cope 1991). The other aspect somewhat contradicts this view in that it emphasizes the increase in small game in Natufian middens compared to earlier Epipaleolithic ones (Bar-El & Tchernov 2000; Stiner & Tchernov 2000). As far as Eynan is concerned, it is apparent that people were hunting, fishing, and collecting every kind of available game. Herbivores other than gazelles were hunted from the Early Natufian on, as were wild boars. From the data at hand, it seems that the contribution of Cervidae and Suidae to human diet increased with time. Waterfowl, hares, and fish suggest the use of snares and nets, but it is difficult at the moment to determine the effective contribution of these species to the total food intake. All in all, there is no evidence for the exclusive hunting of gazelles and, if the pressure on small game is obvious, this may reflect no more than an increase of a previous trend.

But this is not the main point of our discussion; the main point is: what was the impact of man's pressure on natural populations of hunted animals? Was the territory of a given village overexploited? Some of the prey taken by Natufian hunters (hares, for example) are known to reproduce very quickly; others, like migratory birds, are renewed every year. Mountain gazelles are a different case, since they have a relatively low rate of reproduction. Each female bears one fawn a year or slightly more under favorable conditions (Munro 2001:221), and, as non-migratory animals, gazelles are not subject to replacement by foreign populations. It is generally acknowledged that hunted Natufian gazelle populations encompass a higher proportion of immature animals than their earlier counterparts. It is also accepted by many that gazelle populations underwent some reduction in body size compared to older Pleistocene ones, again during the time span of the Natufian culture. Davis (1981, 1983), who first observed these phenomena, understood the increase in immature individuals as a possible result of Natufian sedentism. Sites prior to the Natufian would represent only winter populations, to which new spring-born juveniles would be added by summer hunting in Natufian villages. The size reduction of the animals would be the result of Bergmann's law, which predicts smaller individuals when temperature increases (Davis 1981, 1983).

Further studies by Carol Cope pointed to selective culling of young (immature) males by Natufian hunters. She viewed this as the effect of deliberate control of the herds that she unequivocally termed "proto-domestication." Moreover, she also found a reduction in body size of Natufian gazelles through time but, contrary to Davis, interpreted this as the result of selective killing of males in addition to overexploitation (Cope 1991). According to these findings and the way they were understood, Natufian sedentism and the new control achieved over gazelle herds led to excessive pressure and induced a degenerative process in the animal population. Munro (2001) challenges these conclusions. She agrees that there is a steep increase in immature individuals in Natufian deposits compared to earlier ones: from about 30% to about 50%. But she sees the change as the result of less selective culling of young adults, which were previously the primary target. This induced a relative increase mainly in juveniles but also in old individuals

(Munro 2001:293). The human behavior producing this situation is not clear, but the result is certainly an increase in hunting pressure. According to Munro (2001:300, 304), using population simulation, the pressure went as far as the verge of overexploitation but without reaching that point.

What can we conclude from this discussion? Not every author sees the sexing of gazelles as a very secure procedure (Dayan & Simberloff 1995). Despite this criticism, Tchernov (1997) still maintains that Natufian people began to cull immature male gazelles selectively. To his mind, this practice suggests a close relationship between hunters and herds of herbivores, and it is not by chance that similar behavior is observed among early farmers, millennia later. On the other hand, Ducos & Kolska-Horwitz (1997), in disagreement with the observations of Davis and Cope, note an increase in gazelle body size during the late stages of the Natufian, which they explain as the effect of Bergmann's law when colder conditions prevailed again during the Younger Dryas. But their site sampling is problematic and the issue is complicated by difficulties in ascertaining the extent of the effects of the Younger Dryas in the Southern Levant (see Rossignol-Strick 1997; Sanlaville 1996; Tchernov 1997). Finally, the behavior of the mountain gazelle is far from well documented and will never be so, since there are no longer any wild populations in undisturbed areas. This problem, added to uncertainties about past environments and climates, bears on any population simulation, since the parameters behind it are approximate at best.

For the moment then, it seems difficult to get an accurate idea about the way Natufian hunters exploited their territory. We have abundant data that should not be ignored. These data, generally speaking, point to an interest by Natufian hunters in efficiency in the use of their territory. But concluding there was overexploitation is not warranted. While the change in gazelle hunting habits compared to earlier periods could be a shift to preying on younger males, we are unable to introduce these data securely into a broader theoretical framework.

The notion of ownership

The other questions that I want to address are related to the problem of how people saw their ties to their territory. Did they have any sense of ownership, collective or individual?

As we understand it today, ownership is a juridical concept. In a more general way, it is a relation between two entities, consisting mainly in the interpretation that people give to this relation. In addition, this interpretation should be widely accepted, or people will act to have it accepted. But this concept allows for all kinds of gradations in its different aspects. It is the result of a lengthy historical maturation (see Handman 1991 for a more detailed analysis). So we are facing two difficulties when trying to trace ownership in the past. How are we to identify ownership in the prehistoric record, since ownership is a relation that is in the mind of people? And how are we to recognize the meaning of ownership for those people?

In the Natufian record there are different kinds of data that may suggest some ties between people and objects, people and animals, people and a piece of land. The problem is how to find ways to uncover the meaning that Natufian people gave to these ties. For territories the problem is even more complicated since, as shown before, we are unable to get a clear idea of the item involved in the supposed relation.

I have to say that at this point I cannot see any way to elucidate ownership in the Natufian. The most obvious probable long-term relation of people with objects is shown by the decorative items that are associated with the body of the deceased in the graves. Traces of wear on some of them demonstrate that these decorations were not just made to accompany dead bodies, but were apparently part of daily life (Pichon 1983). Some of these objects are quite elaborate, but what do they tell us about the sense of private property of their bearers? Other objects, like basalt tools, may have involved some sense of ownership, as they are long-lived objects. When found in the context of a house, a close relationship between the inhabitants and the objects is suggested. This was the case for a variety of tools on floors in houses 26 (lower floor and higher floor: Perrot 1966, Figures 10 and 22) and 131 (Valla 1988, Figure 3) at Eynan. But again this does not give any key to understanding the degree of ownership involved. Did the objects belong to the household or to an individual? And what does "belong" really mean in the Natufian context? Some insight into these questions may be offered by the large mortars, some of which look like true masterpieces. Their making implies large amounts of work, if difficult to quantify, and they were probably in use for a long time, possibly for generations. At Eynan, only one of the recovered items is intact, and it was not found *in situ*. But a much simpler mortar made of limestone may exemplify the situation of the basalt objects. According to sections published by Perrot (1966, Figure 13), this mortar may have been in use during two phases of occupation, first in house 26 and later when the house was rebuilt (house 45). When broken fragments of large basalt mortars were found *in situ*, they were in secondary use as building stones in walls (house 51), as blocking elements in post-holes or in the lining of fireplaces (house 131). These are items belonging not to individuals but to "households." By contrast, basalt tools, either usable or broken, are not recorded in graves at this site (as they are elsewhere). Generally speaking, the scarcity of worked objects apart from personal jewelry that were demonstrably placed in graves at Eynan is striking, and jewelry disappears from graves in the Final Natufian layer.

These findings do not allow us to come to any firm conclusions. Only a sense of a collective relation with objects seems to be warranted, and the large mortar in primary position may be an indication of this. The broken reused fragments are more difficult to interpret, since they may simply have been seen as available suitable stones by their users. There are no firm grounds for suggesting individual ownership of the smaller objects. Even the decorative items, which appear to be closely linked to individuals at least through durable bodily contact, hold meaning only from the consensus of the group.

Animal domestication provides another possible avenue of research. Domestication implies a relation of domination, but does this extend necessarily to ownership? Taming a wolf puppy may well indicate a relationship between two individuals, but this relation may range from partnership to ownership. There are two cases, both in graves, where a relation of some form is reflected in the archaeological record. In one of the graves a woman has her hand on the chest of a puppy in a position that suggests power, perhaps ownership, over the animal (Valla 1975–77; see Figure 3). But a glance at the second grave shows that such a conclusion may not be warranted. In this second case, the dog has its hind leg on top of the skull of one of the humans (Valla 1996; see Figure 4). As I have tried to show elsewhere, the arrangements in these graves probably have more to do with mythological beliefs than with everyday life. It is not at the level of these naive observations that we should look for evidence of ownership. More telling is the fact that the dogs were probably killed in order to be buried in the graves. This is a crude expression of domination. Can we go further and identify the level of domination? Was it collective or was it individual? Unfortunately, at the moment I have no answer. The attempt to find out whether sacrifice was involved did not yield any definitive answer because the purpose of the killing could not be securely identified (Valla 2003). This would have contributed to the question of ownership through the relations it suggests between the different actors involved.

Relations between people and a piece of land can be traced at two levels at least: villages and houses. In both cases relations are not between land and an individual but between land and a group of people. Again, in both cases the special relationship between land and people finds its expression in time; or, more precisely, it is the duration of the association that may turn the relation into some kind of feeling of ownership. These ties are expressed in different ways. The work involved in building activity is one of them. Graves have also been cited as a means used by people to stress their rights to a piece of land in case of a dispute (Flannery 1972). If this argument proves correct in the Natufian case, then it provides a good basis for a sense of ownership not far from that of a modern lawyer.

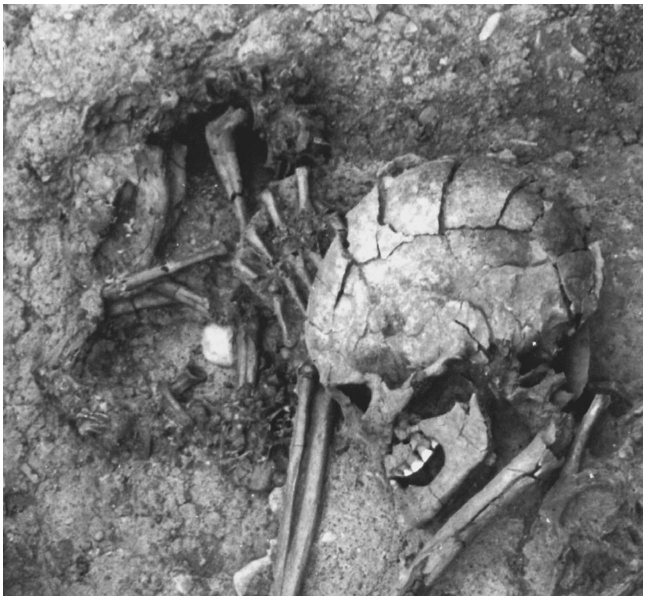

Figure 3. Detail of grave H. 104 at Eynan showing the hand of a woman on the body of a puppy (photo by F. Valla and A. Dagand).

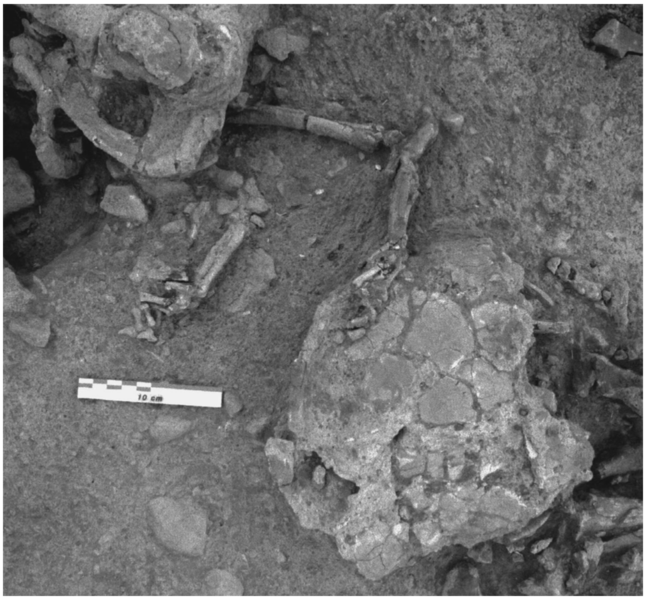

Figure 4. Detail of grave H. 7-8-10 at Hayonim Terrace: note the dog's hind leg on the skull of H. 10 (Photo by F. Valla).

As a matter of fact, however, the data are perhaps not so easy to interpret. In the Near East people are known to have buried their dead in living quarters since the Middle Paleolithic some 100,000 years ago. Graves are not common in Upper Paleolithic deposits but, given the rarity of deposits of this age, they are not so exceptional (e.g., Ohalo II, Nahal En Gev, En Gev I, Kharaneh). The Natufian graves could be part of a long trend that led to some kind of interest in ancestors, as demonstrated by the manipulation of skulls that began in the Natufian, but it is hard to link this practice to a sense of ownership. The association between burials and architecture is clear at Eynan. But how ownership is included in this relation, and what kind of ownership is involved, are hard to elucidate.

At Eynan there are three main occupation levels from Early to Final Natufian. It is not possible with the data at hand to define the duration of these occupations. During each of them the buildings that have been examined show a complicated sequence of construction, abandonment, reorganization, again abandonment, and so on. There are sometimes graves in between these successive phases. These graves demonstrate that the process involved at least years and probably some tens of years. Though the chronological definition is still poor, the time involved clearly allows for ties to grow between the place and its inhabitants. Nevertheless, it also allows for many changes in the composition of the human group and, at the moment, we have no way of knowing what the relation may have been between the users of a specific house over the successive phases of its occupation.

We cannot deal with this problem at the level of the house, since the focus is too narrow. But perhaps we can address it at the level of the village. At a larger scale, the village was occupied in a way that was similar to the houses. In other words, the few indications we have do not point to a continuous occupation of Eynan for two thousand years. On the contrary, the clear-cut geological characteristics of each of the three layers of occupation suggest long periods of abandonment between them. At this level of resolution, however, it seems possible to admit that, at least generally speaking, people coming back to the site shared the same tradition as did their predecessors. This is suggested, for example, by the style of the flint tools that maintains some specificity throughout all three main layers, and by the techniques used to shape the bone tools that again exhibit signs of continuity and distinctiveness compared to other nearby sites. If so, they may well indicate a tie between people and land through time. The fact that people settled at precisely the same place as their predecessors could be another confirmation of these ties.

Discussion

It is time to summarize all these data. We have reached at least three conclusions. First, it is hard to reconstruct the limits of the territory of any given group around a sedentary Natufian site. As a matter of fact, we have no solid basis for recognizing limits and boundaries. The data suggest three zones from which objects were introduced into villages: (1) the nearest zone, some 20–25 km in diameter around the settlement, the source of most items found at the sites; (2) an intermediate zone, more difficult to define, from which relatively few objects were introduced, but which still seems to have relatively steady ties with the sites; and (3) a distant zone with very loose relations to the place, indicated by occasional items.

Second, there are many problems behind our understanding of the way territories around sites were used. The interactions between Natufian hunter-gatherers and their prey are very difficult to ascertain. There are hints that people were trying to get more than their predecessors from the available resources. This apparently prompted them to develop new techniques, probably snares to capture birds and hares, certainly sickles to harvest seeds. But there are also indications that people were not starving or even trying to get every possible type of food. For example, freshwater shells are present but not very abundant in the deposits at Eynan; these resources seem to have been relatively neglected. Partridge is another game animal that was apparently not considered at Eynan. People chose instead to concentrate on waterfowl. It seems that we are at very high risk of circular argument when trying to give broad interpretations of the Natufian fauna because too many uncertainties are involved, both in our knowledge of the animals and in our knowledge of their hunters.

Third, when looking at how people understood their ties to a territory, we face overwhelming difficulties. The consciousness of ownership by Natufian people eludes us at the moment, either because we do not know how to read the evidence at hand, or because the evidence is not explicit enough. We know how to recognize obvious ties between people and objects, people and animals, people and pieces of land. Some of these ties persisted for relatively long periods of time. They may have led to the development of a sense of ownership, but I do not see any way to measure either the nature or the degree of such ownership. Did a collective sense of property emerge? Did individual property come to be acknowledged? The processes involved in these developments remain obscure.

These results may seem very negative, but in fact they are not. In our search we went through quantities of data that served as guides to our investigations. Our questions about territories were probably too specific and too ambitious to expect straightforward answers. Nevertheless, we have gained some insights into Natufian territories and the way they were used. It is not surprising that limits and boundaries elude us. On exploitation versus overexploitation we have plentiful data at our disposal. Finally, examining ownership has led us to what may be a decisive point in understanding Natufian territories. Eynan, as far as we know, was not occupied constantly for the entire length of the Natufian culture. This means that people were able to move to other places, and had the possibility of coming back later. They were probably not confined to a narrow territory that was strictly limited by surrounding territories defended by other groups. Moreover, the situation at Eynan is not peculiar to this site, but is apparently the usual situation. Finally, one could even argue that what happened at the end of the Natufian culture, when every Natufian village was deserted and people eventually settled elsewhere, is another indication that the land was then only loosely occupied. Could it also be an argument to dismiss the endlessly made but never proved claim for population pressure?

It is generally admitted that human population grew at a very slow rate during prehistory. A possible increase in rate is often postulated as a consequence of the beginning of agriculture because of the economic advantage of child labor in the fields (see, for example, Krohne 2001:134). Ever since Binford (1968) suggested population pressure as a possible stimulus for the beginnings of agriculture, speculations have flourished among archaeologists exploring the possible mechanisms leading to population growth in Natufian villages (see Reed 1977 for a theory trying to show that population growth resulted from shorter birth intervals due to sedentism). Other researchers built models combining sedentism, increase in population, and climatic events. Population growth allowed by favorable climatic conditions in Early Natufian villages would ultimately turn into stress when climate deteriorated during the Younger Dryas, leading to manipulation of cereals and eventually to agriculture (Bar-Yosef & Belfer-Cohen 1992). Munro (2001) is the most recent avatar of these models. She advocates population growth accompanying climatic amelioration (forestation) throughout the end of the Pleistocene, leading to sedentism sustained by improved technology in early Natufian villages. An end would have been put to this trend when the "harsh" conditions of the Younger Dryas produced a decline in population, accompanied by more mobility and settling in the desert belt by Late Natufian time. According to this scenario, "the constant resource pressure" of the Natufian period was an incitation to "cereal management," which then led to domestication (Munro 2001:353–354).

Tchernov has already criticized the assumption that cultural development could be stimulated by external inputs such as climate. Moreover, in his view, the "harsh conditions" postulated for the Younger Dryas by those advocating cultural response to environmental pressure are not corroborated by the faunal or speleothem data at hand (Tchernov 1997:221). We listed above some of the evidence supporting the idea that Natufian hunter-gatherers were not using the carrying capacity of the land in full. Munro herself suggests that Late Natufian inhabitants at Hayonim Cave were able to return to a more mobile way of life. This hypothesis seems at logical odds with the assumption that people were limited in space by neighboring groups.

The basic difficulty in these models is the failure to pay serious attention to culture when trying to understand a process that is mainly cultural. According to these points of view, human populations are limited by food scarcity. They tend to reach equilibrium at the highest possible level, given environmental conditions regulated through abiotic agents (like climatic events) that control the carrying capacity of the land. Culture intervenes as a technical means of mediating between carrying capacity and population. Typically, it is understood as forging responses to environmental changes. There is little doubt that these theories are not taking into account the complexity of the phenomena they purport to explain. Even at the level of non-human life, ecologists have long acknowledged the effect of internal biotic phenomena as density regulators. From that point of view the argument advocated by Reed, which includes sedentism as a reason for population growth, is of interest, as is the notion put forward by Cauvin & Cauvin (1982) when they explain that a new organization of hunting may have induced a new form of group organization, which in turn may have allowed larger communities to develop. These approaches at least, if minimally, take into account the internal logic of cultural development.

In his aforementioned paper, Tchernov (1997) refers to the work of Prigogine and suggests (after others) that human societies work like what Prigogine terms "dissipative structures" in the field of thermodynamics. These are structures that are self-organizing and always move towards more and more complexity. They are in a kind of disequilibrium, "extracting energy from their environment" to counteract entropy. As time progresses, this process leads to a point where fluctuations result in a break in the stability of the system, giving rise to unpredictable new organizations at higher levels. Through this process matter acquires new properties, which in turn are irreversible (Prigogine1994:67ff).

These views seem to me much more comprehensive and much more realistic than the oversimplified determinism that lies behind current theories of the origins of agriculture. They emphasize the need to take into account the growing experience of mankind in prehistoric times if we are to understand anything of the development of cultural processes like those leading to villages, towns, and states. Our research programs should be more and more oriented towards these phenomena. We shall probably never be able fully to reconstruct prehistoric social organizations and ways of thinking. But we have much to learn in these fields following the lines already drawn many years ago by A. Leroi-Gourhan, when he started elaborating methods that would allow us to extract ethnographic insights from our data through internal analysis. Demography and population growth will undoubtedly appear along the way in this research. But these phenomena will appear at their appropriate level, included within a wider construct, and not, as it now seems, as a *"deus ex machina"* always at hand to hide our ignorance.

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References

Bar-El, T. & Tchernov, E. (2000). Lagomorph remains at prehistoric sites in Israel and southern Sinai. *Paléorient* **26**, 93–109.

Bar-Yosef, O. (1989). The PPNA in the Levant: An overview. *Paléorient* **15**, 57–63.

Bar-Yosef, O. & Belfer-Cohen, A. (1992). From foraging to farming in the Mediterranean Levant. In (A. B. Gebauer & T. D. Price, Eds.) *Transitions to Agriculture in Prehistory*. Madison, WI: Prehistory Press, pp. 21–48.

Belfer-Cohen, A. (1988). *The Natufian Settlement at Hayonim Cave: A Hunter-gatherer Band on the Threshold of Agriculture*. Unpublished PhD Dissertation, Hebrew University, Jerusalem.

Binford, L. (1968). Post-Pleistocene adaptations. In (S. R. & L. R. Binford, Eds.) *New Perspectives in Archaeology*. Chicago: Aldine-Atherton, pp. 313–341.

Bouchud, J. (1987). Les mammifères et la petite faune du gisement Natoufien de Mallaha (Eynan). In (J. Bouchud, Ed.) *La Faune du Gisement Natoufien de Mallaha (Eynan)*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem 4. Paris: Association Paléorient, pp. 1–150.

Cauvin, J. & Cauvin, M.-C., (1982). Origines de l'agriculture au Levant: Facteurs biologiques et socio-culturels. In (T. C. Young, P. E. L. Smith & P. Mortensen, Eds.) *The Hilly Flanks, Essays on the Prehistory of Southwestern Asia Presented to Robert J. Braidwood*. Studies in Ancient Oriental Civilization 36. Chicago: The Oriental Institute, pp. 43–55.

Cauvin, M.-C. (1991). L'obsidienne au Levant préhistorique, provenance et fonction. *Cahiers de l'Euphrate* **5–6**, 163–190.

Cope, C. (1991). Gazelle hunting strategies in the southern Levant. In (O. Bar-Yosef & F. R. Valla, Eds.) *The Natufian Culture in the Levant*. Ann Arbor: International Monographs in Prehistory, pp. 341–358.

Davis, S. J. M. (1981). The effect of temperature change and domestication on the body size of late Pleistocene to Holocene mammals of Israel. *Paleobiology* **7**, 101–114.

Davis, S. J. M. (1983). The age profiles of gazelles predated by ancient man in Israel: Possible evidence for a shift from seasonality to sedentism in the Natufian. *Paléorient* **9**, 55–62.

Dayan, T. & Simberloff, D. (1995). Natufian gazelles: Proto-domestication reconsidered. *Journal of Archaeological Science* **22**, 671–675.

Delage, C. (2001). *Les Ressources Lithiques dans le Nord d'Israël: La Question des Territoires d'Approvisionnement Natoufiens Confrontée à l'Hypothèse de la Sédentarité.* Thèse de Doctorat Non-publiée. Paris: Université de Paris I.

Dimentman, Ch., Bromley, H. J. & Por, F. D. (1992). *Lake Hula: Reconstruction of the Fauna and Hydrobiology of a Lost Lake.* Jerusalem: The Israel Academy of Sciences and Humanities.

Ducos, P. & Kolska-Horwitz, L. (1997). The influence of climate on artiodactyl size during the Late Pleistocene-Early Holocene of the Southern Levant. *Paléorient* **23**, 229–247.

Edwards, P. C. (1991). Wadi Hammeh 27: An Early Natufian site at Pella, Jordan. In (O. Bar-Yosef & F. R. Valla, Eds.) *The Natufian Culture in the Levant*. Ann Arbor: International Monographs in Prehistory, pp. 123–148.

Flannery, K. V. (1972). The village as a settlement type in Mesoamerica and the Near-East: A comparative study. In (P. J. Ucko, R. Tringham & G. W. Dimbleby, Eds.) *Man, Settlement and Urbanism.* London: Duckworth, pp. 23–53.

Handman, M.-E. (1991). Propriété. In (P. Bonte & M. Izard, Eds.) *Dictionnaire de l'Ethnologie et de l'Anthropologie.* Paris: Presses Universitaires de France, pp. 605–606.

Henry, D. O. (1975). Fauna in Near Eastern archaeological deposits. In (F. Wendorf & A. E. Marks, Eds.) *Problems in Prehistory: North Africa and the Levant*. Dallas: Southern Methodist University Press, pp. 379–385.

Krohne, D. T. (2001). *General Ecology*. Pacific Grove: Brooks/Cole.

Lechevallier, M. (1978). *Abou Gosh et Beisamoun. Deux Gisements du VIIe Millénaire Avant l'Ere Chrétienne en Israël.* Mémoires et Travaux du Centre de Recherche Français de Jérusalem 2. Paris: Association Paléorient.

Mienis, H. K. (1987). Molluscs from the excavation of Mallaha (Eynan). In (J. Bouchud, Ed.) *La Faune du Gisement Natoufien de Mallaha (Eynan), Israël*. Mémoires et Travaux du Centre de Recherche Français de Jérusalem 4. Paris: Association Paléorient, pp. 159–177.

Moore, A. M. T. (1991). Abu Hureyra 1 and the antecedents of agriculture on the Middle Euphrates. In (O. Bar-Yosef & F. R. Valla, Eds.) *The Natufian Culture in the Levant*. Ann Arbor: International Monographs in Prehistory, pp. 277–294.

Munro, N. D. (2001). *A Prelude to Agriculture: Game Use and Occupation Intensity during the Natufian Period in the Southern Levant.* Unpublished PhD Dissertation, University of Arizona, Tucson.

Perrot, J. (1966). Le gisement Natoufien de Mallaha (Eynan), Israël. *L'Anthropologie* **70**, 437–484.

Pichon, J. (1983). Parures Natoufiennes en os de perdrix. *Paléorient* **9**, 91–98.

Prigogine, I. (1996). *La Fin des Certitudes: Temps, Chaos et les Lois de la Nature.* Paris: Odile Jacob.

Reed, C. (1977). The origins of agriculture: Prologue. In (C. Reed, Ed.) *Origins of Agriculture.* The Hague: Mouton, pp. 9–21.

Reese, D. S. (1991). Marine shells in the Levant: Upper Palaeolithic, Epipaleolithic and Neolithic. In (O. Bar-Yosef & F. R. Valla, Eds.) *The Natufian Culture in the Levant*. Ann Arbor: International Monographs in Prehistory, pp. 613–628.

Rossignol-Strick, M. (1997). Paléoclimats de la Méditerranée orientale et de l'Asie du Sud-Ouest de 15.000–6.000 B.P. *Paléorient* **23**, 175–186.

Sanlaville, P. (1996). Changements climatiques dans la région Levantine à la fin du Pléistocène supérieur et au début de l'Holocène: Leurs relations avec l'évolution des sociétés humaines. *Paléorient* **22**, 7–30.

Stiner, M. C. & Tchernov, E. (1998). Pleistocene species trends at Hayonim Cave: Changes in climate versus human behaviour. In (T. Akazawa, K. Aoki & O. Bar-Yosef, Eds.) *Neandertals and Modern Humans in Western Asia*. New York: Plenum Press, pp. 241–262.

Tchernov, E. (1997). Late Pleistocene environmental factors, faunal changes and cultural transformations: The case of the Southern Levant. *Paléorient* **23**, 208–228.

Tchernov, E. & Kolska-Horvitz, L. (1990). Herd management in the past and its impact on the landscape of the Southern Levant. In (S. Bottema, G. Entjes-Nieborg & W. van Zeist, Eds.) *Man's Role in Shaping the Eastern Mediterranean Landscape*. Rotterdam: Balkema, pp. 207–216.

Valla, F. R. (1975–77). La sépulture H. 104 de Mallaha et le problème de la domestication du chien en Palestine. *Paléorient* **3**, 287–292.

Valla, F. R. (1988). Aspects du sol de l'abri 131 de Mallaha (Eynan). *Paléorient* **14**, 283–296.

Valla, F. R. (1996). L'animal "bon à penser": La domestication et la place de l'homme dans la nature. In (M. Otte, Ed.) *Nature et Culture*. Liège: ERAUL 68, pp. 651–667.

Valla, F. R. (2003). Une urgence: Donner du sens. Des sacrifices dans le Natoufien et l'horizon PPNA du Proche-orient Levantin? In (Collectif) *Sens Dessus Dessous: La Recherche du Sens en Préhistoire. Recueil d'Etudes Offert à Jean Leclerc et Claude Masset*. Revue Archéologique de Picardie, Numéro Spécial, pp. 205–218.

Valla, F. R., Khalaily, H., Samuelian, N., Bocquentin, F., March, R., Valentin, B., Marder, O., Rabinovich, R., Le Dosseur, G., Dubreuil, L. & Belfer-Cohen, A. (2001). Le Natoufien final de Mallaha (Eynan), deuxième rapport préliminaire: Les fouilles de 1998 et 1999. *Journal of the Israel Prehistoric Society* **31**, 43–184.

Weinstein-Evron, M., Kaufman, D. & Bird-David, N. (2001). Rolling stones: Basalt implements as evidence for trade/exchange in the Levantine Epipaleolithic. *Journal of the Israel Prehistoric Society* **31**, 25–42.

Few areas of the world have played as prominent a role in human evolution as the Levantine Corridor, a comparatively narrow strip of land sandwiched between the Mediterranean Sea on the west and the expanse of inhospitable desert to the east. The earliest hominids to leave Africa, over 1.5 million years ago, first entered the Levant before spreading throughout the rest of Eurasia. About 100,000 years ago another African exodus, this time of anatomically modern humans, colonized the Levant before expanding into Eurasia. Toward the end of the Pleistocene the Corridor also witnessed some of the earliest steps toward economic and social intensification, perhaps the most radical change in human lifeways that ultimately gave rise to sedentary communities wholly dependent on domestic animals and cultivated plants.

Why has the Levantine Corridor been so important in the unfolding story of human evolution? This book, which grew out of an interdisciplinary project on the "Paleoecology of the Levantine Corridor" sponsored by the Institute for Advanced Studies of the Hebrew University of Jerusalem, looks at the complex interplay between the Levant's dynamic tectonic and environmental history and the changing lifeways of the humans who inhabited the region over the course of the Pleistocene. Readers will find here a rich diversity of contributions that explore the paleoecology of the Levantine Corridor and the myriad ways in which its inhabitants – both human and non-human – have responded and adapted to this ever-changing landscape.

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